# TAXONOMIC AND ECOLOGICAL STUDIES OF THE TASMANIAN *EUCALYPTUS*-DEFOLIATING PAROPSIDS (COLEOPTERA:CHRYSOMELIDAE), WITH PARTICULAR REFERENCE TO *CHRYSOPHTHARTA BIMACULATA* (OLIVIER)

by

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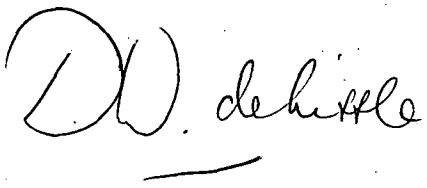
This thesis contains no material which has been accepted for the award of any other degree of diploma in any university, and to the best of the author's knowledge, contains no copy or paraphrase of material previously published or written by any other person except where due reference is made in the text of the thesis.



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Female *Chrysophtharta agricola* (Chapuis) ovipositing on juvenile leaf of *Eucalyptus globulus* Labill. grown in plantation in N.W. Tasmania by Associated Forest Holdings Pty. Ltd.

"The complexity of the organic world is enormous and naturally frustrates the inquiring mind. So enormous is the number of organisms, so infinite their many and varied relationships, so subtle and far-reaching are the influences of their constant activity and evolving natures, as to laughingly belittle those persons who, usually lacking an extensive familiarity with the phenomenon, think that they will manufacture simple models of the system to facilitate their understanding. Physicists badger the fundamental material of the universe in their attempts to understand the complexities of the interaction of some fifty "elementary particles", an enormous task. Would you care to try to understand the possible interactions and relationships to other living things of 300,000 species of beetles?".....

"Not only is the natural world complex beyond imagination, it also eludes understanding (not, I hope, appreciation) because it is constantly changing; the ecologist enters this shifting matrix at his own risk. Some delineate small aspects of the ecological theatre; others carefully investigate small parts of the evolutionary play. No man can encompass the entire performance."

Daniel C. Kozlovsky,

"An Ecological and Evolutionary Ethic"

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SUMMARY

This study investigates the taxonomy and ecological relationships of the Tasmanian *Eucalyptus*-defoliating paropsid beetles of the family Chrysomelidae. In particular, the host-plant relationships, life history and population ecology of *Chrysophtharta bimaculata* (Olivier) a major forest pest in Tasmania, are investigated.

A survey of eucalypt forest and woodland over much of the island revealed the presence of at least thirty-six paropsid species which fed on the foliage of eucalypts. These species belonged to five genera, *viz*: *Paropsis* Olivier (*sensu stricto*) (nine species), *Trachymela* Weise (eight species), *Chrysophtharta* Weise (thirteen species), *Paropsisterna* Motschulsky (three species) and *Sterromela* Weise (three, or possibly four species).

All species were described and indicated by a code, but it was only possible to positively identify twenty-three species. No attempt was made to name new species, since it was considered that in the absence of a recent revision of the entire paropsid fauna, this would only serve to increase nomenclatural confusion within the group. Keys to adults and fourth instar larvae are provided. Records of *Eucalyptus* species on which each species of *Paropsis* was found at each collecting locality are given. The Tasmanian island paropsid fauna on eucalypts is compared and contrasted to that of mainland Australia in the light of current limited knowledge.

Ecological relationships of the more common paropsids are discussed in relation to r and K strategy and niche differentiation. The host-plant relationships of two very common, highly r-selected species, *Chrysophtharta bimaculata* and *C. agricola* (Chapuis) were studied in detail in the field, insectary and laboratory.

*C. bimaculata* showed a field preference for *Monocalyptus* species of the series Obliquae, while *C. agricola* preferred *Symphyomyrtus* species. In laboratory larval feeding trials, *C. bimaculata* performed better on a *Monocalyptus* species (*E. delegatensis*) than on a *Symphyomyrtus* species (*E. dalrympleana*) while *C. agricola* performed equally well on both species. *C. bimaculata* developed faster but was a less efficient feeder than *C. agricola* on *E. delgatensis*. It was therefore inferred that *C. bimaculata* was more highly r-selected than *C. agricola*, competitively displacing the latter species from *E. delegatensis*.

Detailed studies were made of the life history and population ecology of *C. bimaculata*. This species was shown to be univoltine at least in N.W. Tasmania,and not bivoltine as previously considered. Partial population budgets were prepared for three populations. A major mortality factor in populations of immature *C. bimaculata* was the predatory coccinellid, *Cleobora mellyi* Mulsant which accounted for up to 74 percent of egg mortality. Egg parasitization and larval parasitization by the braconid species *Eadya paropsidis* were described for the first time. The pest potential of *C. bimaculata* is discussed in the light of its host-plant relationships, ecological strategies of its preferred hosts, and other population determinants.

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# SECTION I - INTRODUCTION

## INTRODUCTION

The uniquely Australian tree genus, *Eucalyptus*, contains a great number of species which have successfully colonized virtually every climatic zone in Australia, and which constitute the dominant vegetation in many areas. The paropsids, which are a large group in the cosmopolitan family of leaf-eating beetles, the Chrysomelidae, have successfully occupied defoliating niches on the species of *Eucalyptus*, and also on species of some other myrtaceous genera and *Acacia*. With the intensive cultivation of eucalypts for timber and for paper pulp in recent years in Australia, both in natural regeneration and in plantations, some paropsid species have emerged as significant pests. In New Zealand, where eucalypts have been grown for many years, the introduced paropsid, *Paropsis charybdis* Stål has been a major pest since it was first recorded in the Canterbury district in 1916.

The island of Tasmania, with its geologically recent isolation from, but close biogeographic affinities to the Australian mainland, provides an ideally defined region for the study of a small sub-set of the *Eucalyptus*-defoliating paropsid fauna. The aims of the present study were threefold, *viz*:

1) to identify the paropsid species occurring in Tasmania on eucalypts, and to prepare simple keys for their recognition;

2) to investigate reasons for the relative abundance and host preferences of some of the more common species; and

3) to study in detail the life history and population ecology of a species of major pest status (*Chrysophtharta bimaculata*) which attacks the commercially preferred eucalypt species in Tasmania.

With few exceptions, very little taxonomic and ecological research on the Australian paropsids has been undertaken to date. This study has attempted to provide factual information on these two aspects through descriptive, qualitative and semi-quantitative methods, in a number of natural habitats, and through laboratory studies. The relative status of the Tasmanian paropsids has been assessed, and factors involved in host-plant selection and population regulation have been broadly outlined.

# SECTION II - LITERATURE REVIEW

# 1. The *Eucalyptus*-defoliating paropsid beetles; their taxonomy; and the biogeographical relationship of the island of Tasmania to the Australian continent

## 1.1. The paropsid chrysomelids

The *Eucalyptus*-defoliating paropsid beetles belong to the family Chrysomelidae, species of which are commonly known as leaf beetles because of their leaf-feeding habit. The Chrysomelidae is cosmopolitan in distribution, and is one of the five largest families of the Coleoptera in terms of species numbers. In the Australian fauna, it is among the three most numerously represented of the coleopterous families (Britton 1970). Of the ten subfamilies of the Chrysomelidae which are represented in Australia, the subfamily Chrysomelinae is mainly represented by the very large paropsid group including the genus *Paropsis* Olivier and allied genera. Species of this group feed as adults and larvae mainly on species of the large plant genus *Eucalyptus* (family Myrtaceae), but also on the allied genera *Angophora*, *Tristania*, *Leptospermum* and *Melaleuca*, as well as on *Acacia* (family Leguminosae) (Cumpston 1939; B.J. Selman *pers. comm.*).

## 1.2. The species concept in the family Chrysomelidae

Mayr (1963) defined zoological species as "groups of interbreeding natural populations that are reproductively isolated from other such groups". This definition was derived from the biological species concept which, together with the typological and nominalistic species concepts were discussed in detail by Mayr (1969). Although reproductive isolation is not directly

observable, it can be inferred from morphological characteristics, since the isolation of the gene pool of species results in a discontinuity not only of the genotype, but also of the resultant phenotype.

When species are investigated in the context of time, and, in particular, of space, morphological discontinuities between them are frequently difficult to recognize due to the existence of considerable ranges of intra-specific morphological variation. This has led to the definition of subspecies and polymorphic forms. Mayr (1969) defined a subspecies as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species". Polymorphism was defined as "the simultaneous occurrence of several discontinuous phenotypes or genes in a population, with the frequency even of the rarest type higher than can be maintained by recurrent mutation" (Mayr *loc. cit.*). Hence, while polymorphic forms frequently occur sympatrically, subspecies usually represent the different allopatric forms of a species.

In a review of taxonomic problems with closely related species of insects, Brown (1959) suggested that species had three attributes of taxonomic importance: their physiological and morphological differences, and their natural occurrence as discrete entities. Field ecological studies revealed information about physiological differences and natural occurrences, while morphological studies were usually made on preserved specimens. The preserved sample should therefore be random, include all stages, and be comprehensive enough to show the range of variation and frequencies of the variants within the population.

The problem of taxonomic definitions of species and infra-specific forms was summarized by Brown (*loc. cit.*) thus:

> "The simple binomial or trinomial nomenclature cannot depict the great variety of situations that taxonomists perceive, and taxonomists perceive only the more obvious of the situations. Consequently, the best taxonomic arrangements are greatly over simplified."

The Chrysomelidae have long been recognized as a difficult group taxonomically, due to the common occurrence of sibling species (biological species which are morphologically difficult to separate). Brown (1959) stated:

> "In the chrysomelid genera that feed on leaves in the larval stage ..... there is a high degree of host specificity. This furnishes the only known basis for segregating some of the species, although slight, often inconstant morphological differences can usually be detected after the species have been distinguished."

In reviewing the North American chrysomeline genera *Calligrapha, Phytodecta, Phratora, Chrysomela* and *Chrysolina* Brown (1942, 1945, 1951, 1956, 1962) worked out much of the taxonomy in the field and in the laboratory. The most effective isolating factors between species and subspecies were their host-plants and their distribution. For example, within the *Chrysomela interrupta* F. complex, Brown (1956) identified sibling species and subspecies which fed on different species of *Alnus, Populus* and *Salix* in different regions of the North American sub-continent.

## 1.3. Taxonomic history of the Australian paropsids

The generic name "Paropside" or, in the latinized Greek form, *Paropsis*, meaning a dish, was first given to a group of Australian chrysomelids by Olivier (1807) who described these insects, in general terms, thus:

> "These insects have, indeed, an oval or more often rounded form, flat below, a little convex above, resembling, for the most part, the coccinellids, with which it is still not possible to confuse them, due to the length of the antennae and of the number of tarsal segments." (Author's translation.)

Several species placed by Olivier (*loc. cit.*) in *Paropsis* had already been described by Fabricius (1787, 1801) in the genus *Chrysomela* L., including two species collected in Tasmania. These were *Paropsisterna morio* (F.) collected by the Cook expedition of 1777 and *P. rufipes* (F.) collected by the D'Entrecasteaux expedition of 1792.

The same group of leaf beetles was also independently known to Marsham (1808) who described them under the generic name *Notoclea*. Latreille (1807) described the genus *Coccinelloides* a few months before Olivier's description of *Paropsis*, but based his description on one species only, *C. australasiae* (F.), which was also included in the description of *Paropsis*. Selman (1963) has pointed out that although this would appear to synonymize the two genera, no specimens of *C. australasiae* have survived, and the species is unidentifiable from descriptions. *C. australasiae* was therefore a *nomen dubium* and *Coccinelloides* Latreille a valid genus founded on a single, doubtful species.

As Australia was explored and settled throughout the nineteenth century, many new species of *Paropsis* were described by European taxonomists from material forwarded by Australian collectors. Erichson (1842) described twelve new *Paropsis* species from among insect specimens collected at "Woolnorth" in the far north west of Van Diemens Land (Tasmania).

Attempts to split the large genus into a number of smaller genera were made by Motschulsky (1860) and Baly (1864). The latter author split *Paropsis* into two groups: species with irregular elytral puncturation and species with elytral puncturation arranged in ten rows; however, a review of the first group only was published.

*Paropsis* (*sensu lato*) was first fully reviewed by Chapuis (1877) who described 94 new species making a total of 226 described species. Chapuis split the genus into four groups based primarily on elytral puncturation. Blackburn (1894, 1896, 1897, 1898a, 1898b, 1899, 1901), in his revision of the genus *Paropsis* (*sensu lato*), followed and extended Chapuis' system of classification.

Weise (1901, 1908, 1915) split *Paropsis* into a number of genera, retaining three of Motschulsky's (1860) genera (*Paropsisterna*, *Dicranosterna* and *Paropsides*) and erecting eight new genera (*Chrysophtharta*, *Trachymela*, *Sterromela*, *Trochalodes*, *Pyrgo*, *Faex*, *Philhydronopa* and *Procris*). *Paropsis* Olivier was redefined (Weise 1901) to include only those species comprising Baly's (1864) first division and Chapuis' (1877) and Blackburn's (1901) group one. The twelve resulting genera, together with one South American genus, were incorporated into two tribes, the *Dicranosternini* and the *Paropsini*, based on the presence or absence of cilia on the

epipleuron, by Weise (1915). Weise (1916), in the Coleopterorum Catalogus, listed a total of 404 species occurring in Australia, in these two tribes. Forty species were listed as occurring in Tasmania. Lea (1903) also listed forty paropsid species in Tasmania.

The first and only published descriptions of immature stages were prepared by Cumpston (1939) who described eggs, larvae and pupae of four species of *Paropsis*, one of *Chrysophtharta* and two of *Paropsisterna*. The species described were all from south east Australia, and common to the Canberra and Sydney areas. Larval descriptions were based largely on the body tubercle pattern in its progressive modifications throughout the four larval instars, patterns of aggregation of larvae, and coloration of the final instar larvae.

Selman (1963), in a reappraisal of *Paropsis* (*sensu stricto*), concluded that the nomenclature of the species included in this genus was in many cases extremely confused, because past authors had seldom examined type specimens and many incorrect synonymies had resulted. *P. obsoleta* Olivier was selected as the type species for the genus, as Motschulsky's (1860) designation of *P. variolosa* (Marsham) was invalid.

## 1.4. Biogeographical relationships of Tasmania to Australia with particular reference to the genus *Eucalyptus*

The unique features of island biota have been recognized for some time, and theoretical aspects were studied in detail by Macarthur and Wilson (1967). Williams (1974) summarized the relationship of the island of Tasmania to the Australian mainland

with respect to the origin of biogeographical differences and similarities as follows:

> ".... Firstly, and in strong contrast to the Australian mainland, the driest of all inhabited continental land masses, Tasmania is well-watered and has a more temperate and equable climate. One important reflection of this is the abundance of permanent fresh-water streams and lakes *vis-a-vis* the mainland. Secondly, Tasmania is the only part of Australia with significantly large areas that were glaciated during the Pleistocene (only a very small part of the Australian mainland, the highest, was subject to Pleistocene glaciation). Thirdly, although Tasmania is presently separated from the mainland by Bass Strait, a substantial marine barrier, this has been bridged in times past, and the total biogeographical and ecological effect of the strait has been both as a biological 'filter' and barrier. Thus, as a result of the insularity as well as the climate and natural position of Tasmania as the region furtherest from the Indonesian Archipelago - an important invasion route for much of the Australian biota - there remains there a strong "Antarctic" biotic element, and the diversity of several groups on the island is high relative to the mainland. If Australia's interesting and unique biota can be said to result from the remote geographical position and insularity of Australia, then this feature is further heightened in Tasmania, its most remote and isolated part." (pp. 3-4).

Bass Strait appears to have been open during the Miocene, but was in all probability closed during part of the Pliocene when a land bridge extended from Wilson's Promontory through the islands of the Furneaux Group to N.E. Tasmania. The Strait was open and closed periodically during the Pleistocene, in accordance with fluctuating sea levels (Williams *loc. cit.*). Jennings (1971) has placed the final point of severance from the mainland at the Wilson's Promontory - Flinders Island link; this severance occurring at a date of 12,000 - 13,500 BP.

The natural vegetation of Tasmania was described by Jackson (1965) who noted that, in spite of the temperate oceanic climate, it was varied due to the mixture of Australian and Southern Oceanic ("Antarctic") components, and a wide diversity of habitats. The three main ecological formations represented were austral-montane, temperate rain forest, and sclerophyll forest; however, the widespread occurrence of edaphic and fire determined disclimaxes preventing full expression of the climate, resulted in many sub-forms ecotonal between these main formations. The sclerophyll forest was completely dominated by trees of the genus *Eucalyptus*, however, an important ecotonal disclimax sub-formation was wet sclerophyll forest, in which *Eucalyptus* was normally over-dominant and rainforest species (mainly *Nothofagus cunninghamii*(Hook). Oerst. and *Atherosperma moschatum* (Labill.) formed an understorey.

Jackson (*loc. cit.*) mapped the distribution of the species of *Eucalyptus* occurring in Tasmania, and considered that they showed a mosaic distribution correlated with aspect, soil type and altitude. The classification of the Tasmanian eucalypts,

according to the system proposed by Pryor and Johnson (1971) is as follows:-

| Subgenus | Section | Series | Subseries | No. of Species | | |
|---|---|---|---|---|---|---|
| | | | | Total | Tas. | Tas. Endemic |
| Monocalyptus | Renantheria | Obliquae | Obliquinae | 5 | 1 | |
| | | | Delegatensinae | 3 | 1 | |
| | | | Regnantinae | 4 | 1 | |
| | | | Considenianinae | 7 | 1 | |
| | | | Pauciflorinae | 6 | 1 | |
| | | Piperitae | Amygdalininae | 14 | 6 | 5 |
| Symphyomyrtus | Maidenaria | Ovatae | Ovatinae | 12 | 3 | 2 |
| | | Viminales | Globulinae | 18 | 1 | |
| | | | Vernicosinae | 1 | 1 | 1 |
| | | | Viminalinae | 11 | 1 | |
| | | | Cordatinae | 25 | 7 | 5 |

Endemism is high in taxa well represented in Tasmania, and several non-endemic species occurring in Tasmania have a limited distribution in mainland south east Australia. Jackson considered the wholly endemic groups, and the relict distributions of species with mainland affinities, indicated periods of isolation and reciprocal invasion during the Pleistocene.

## 2. The role of paropsid grazers in eucalypt forest ecosystems

### 2.1. Insect grazers as regulators of forest ecosystems

The traditional viewpoint of tree defoliation by insects has been one of "growth impact" (Graham and Knight 1965; Kulman 1971). Kulman considered that the major components of growth impact consisted of mortality, growth loss, rotation delays and increased susceptibility to secondary insects and disease. When making quantitative statements of foliage loss it was necessary to take into account factors pertaining to the physiological status of the tree and the condition and location of the foliage. Rafes (1970) suggested that increment losses alone may be an inadequate measure of the overall response of the forest ecosystem to defoliation. Although difficult to categorize all the effects of insect activity as either detrimental or beneficial to the ecosystem, attempts to interpret their significance in relation to other components and processes of the system were necessary.

Mattson and Addy (1975) drew attention to the concept that insects could act as regulators of primary production and nutrient cycling, and thus perform a vital function in forest ecosystem dynamics. They noted that most studies were carried out during outbreak conditions of a particular pest, were short term, and consequently attention was focussed on the immediate increment loss aspect. However, a few long-term studies showed that insect grazers performed a regulatory function in forest primary production, in that their actions appeared to vary inversely with the vigour and productivity of the system. The interactions

of host age, stress, low site fertility and availability of nutrients led to increases in quality of host food and decreases in host resistance. These changes enhanced insect survival and fecundity. The initial result of increased defoliation was a change in the distribution and relative availability of the abiotic flux for the tree system, but the ultimate result might be a recharge of the cycling nutrient pool.

Estimates of rates of insect grazing in forest ecosystems are scarce. Mattson and Addy (*loc. cit.*) considered that normal insect grazing of from 5 to 30 percent of annual foliage crops usually did not impair plant production, and could even accelerate growth. Burdon and Chilvers (1974a, b) estimated normal rates of defoliation in eucalypt forests of S.E. Australia to vary between 10 and 30 percent, while Springett (1978) proposed a range of 15 to 30 percent for W. Australian eucalypt forests.

Springett (*loc. cit.*) proposed that eucalypt forests were unique among forests because the normal levels of insect defoliation they experienced were significantly higher than in other forests. This implied that more regulation was required in eucalypt forests than in other forests, due possibly to the fact that under relatively erratic climatic and poor edaphic conditions, eucalypts had evolved extremely efficient autotrophic exploitation mechanisms.

## 2.2. General effects of defoliation on eucalypts

Variation in sapwood starch levels in some eucalypts and *Angophora costata* (Gaertn.) J. Britt., in relation to season and regeneration after defoliation, were investigated by Bamber and

Humphreys (1965). These authors considered that since starch was the principal storage carbohydrate in most hardwoods, and was a source of sugars for plant growth and respiration, the amounts of starch may bear some relationship to the ability of a tree to survive such calamities as defoliation due to bushfire or plagues of leaf-eating insects. A reduction in starch was generally found during winter, and highest levels were present in spring and early summer. Reduction in starch levels was significantly greater during the period of tree crown regeneration following defoliation than the normal seasonal reduction.. Since nil starch content was recorded in trees which died following defoliation, death could have been due to the exhaustion of starch to a level at which, in the absence of photosynthetic foliage, growth and respiration were not supported.

Cremer (1972, 1973), in experiments with regeneration of *Eucalyptus regnans* F. Muell., *E. obliqua* L'Herit. and *E. delegatensis* R.T. Bak. in Tasmania, found that recovery from complete defoliation was best in late winter or spring, and poorest in late summer or autumn. A single removal of leaves or axillary buds from the top or middle of 2-8m *E. regnans* crowns had little to no effect on height growth; however, weekly removal resulted in a substantial reduction in height growth. Removal of both leaves and axillary buds from the top of the young trees had a still greater retarding effect on height growth, but when the apical bud was also removed, the retardation was most severe. Recovery after disbudding was found to involve the release of accessory axillary buds, which took place even in the presence of leaves and the apical bud. It was therefore concluded (Cremer

1972) that disbudding or defoliation of the top 40cm of *E. regnans* saplings is not likely to impair height growth unless these injuries are combined, or recurring.

## 2.3. The major insect defoliators of eucalypts

Greaves (1967), Newmann and Marks (1976) and Carne and Taylor (1978) have reviewed the major defoliating insects in Australian commercial eucalypt forests.

The phasmatids *Didymuria violescens* (Leach) and *Podocanthus wilkinsoni* (Macleay) cause serious defoliation to stands of *E. regnans* and *E. delegatensis* in S.E. Australia (Campbell 1961, 1964; Readshaw 1965; Mazanec 1966, 1967, 1968; Readshaw and Mazanec 1969).

Paropsid leaf beetles, and Christmas beetles (scarabs) are serious pests of regeneration, plantations and mature forests (Carne 1966; Carne *et al.* 1974; Greaves 1966; Kile 1974; de Little and Madden 1976; P.B. Carne, unpubl. report).

Other serious defoliators of more restricted occurrence are lepidopteran caterpillars including the jarrah leaf miner, *Perthida glyphopa* Common (Wallace 1970; Mazanec 1974, 1978), the gum leaf skeletonizer, *Uraba lugens* (Walker) (Campbell 1962, 1971; Morgan and Cobbinah 1977) and the autumn gum moth, *Mnesampela privata* (Guen.)(Elliott and Bashford 1978). The sawfly, *Perga affinis affinis* Kirby, is a defoliator of minor importance on eucalypts (Carne, 1962, 1965, 1969).

## 2.4. The effects of paropsid defoliation

Extensive defoliation of plantation grown eucalypts, particularly *E. grandis* Hill ex Maid. in northern coastal New South Wales, is largely due to the Christmas beetle, *Anoplognathus*

*chloropyrus* (Drapiez) and *A. porosus* (Dalman), and the paropsid, *Chrysophtharta cloelia* (Stål) (Carne *et al.* 1974; P.B. Carne, unpubl. report). Defoliation due to *C. cloelia* is considerably more damaging than *Anoplognathus* defoliation. While *Anoplognathus* spp. feed on foliage only as adults, and early in the season, allowing trees to refoliate and store reserves prior to winter, *C. cloelia* feed as both larvae and adults from early summer to late autumn. Trees defoliated by *C. cloelia* are therefore unable to build up carbohydrate reserves prior to winter. While a defoliation level of below 50 percent due to *Anoplognathus* spp. was considered unlikely to reduce the rate of tree growth, *C. cloelia* frequently destroyed apical buds, with a consequent severe reduction in growth increment, and the production of many lateral branches giving an undesirable growth form. Carne (1966) reported occasional death of woodland eucalypts in S.E. Australia due to defoliation by adults and larvae of the paropsid *Paropsis atomaria* Olivier. Active defoliation by this beetle occurs from late spring until early winter.

In Tasmania, the paropsid *Chrysophtharta bimaculata* (Olivier) has been regarded as the major defoliating pest of forest eucalypts (P.B. Carne, unpubl. report). Severe defoliation of *E. regnans* regeneration in the Florentine Valley of southern central Tasmania was reported by Greaves (1966), and of mature (60 year-old) *E. regnans* and *E. obliqua* in southern Tasmania, by Kile (1974). Heavy defoliation of *E. delegatensis* regeneration and mature trees has been reported by D. de Boer (*pers. comm.*) and K.L. Taylor (*pers. comm.*). Greaves (*loc. cit.*) considered

that the most noticeable effect of defoliation caused by *C. bimaculata* was on height growth. When trees were protected from defoliation by continual spraying with insecticide during a season in which there was a high population of *C. bimaculata*, mean height increments of these trees, measured the following winter, were approximately twice as great as the mean height increments of unsprayed control trees.

Apart from the direct effects of growth loss, it has been suggested that paropsid defoliation may predispose eucalypts to attack by other organisms by contributing towards a condition of stress in the host trees. Kile (1974) considered a partial defoliation of mature *E. regnans* and *E. obliqua* by *C. bimaculata* could be a factor contributing to the 'dieback' condition observed in those trees in S. Tasmania. Increased susceptibility of eucalypts to attack by psyllids, coccids and cossid, hepialid and cerambycid wood borers was considered possible by P.B. Carne (unpubl. report). Carne suggested that increased susceptibility of *E. grandis*, planted on old farmlands, to defoliation by *C. cloelia*, may be due to a stress condition induced in the trees by competing grasses. This is consistent with Mattson and Addy's (1975) suggestion that physiological stress may affect attractiveness of trees to specific insects by an alteration of their "chemical halo" (Hanover 1975).

## 3. The ecology of grazing insects with special reference to the paropsids

### 3.1. Adaptive and defensive strategy and behaviour of grazing insects

Kennedy (1953) suggested that "the host plant is not merely something fed on, it is something lived on". A consequence of adaptation to a food source of inherent low nutrient quality, such as plant foliage, is that much of the grazing insect's life is spent feeding, in order to ingest sufficient nutrients for adequate growth, development, and reproductive success (Southwood 1973).

#### 3.1.1. Seasonal Strategies

In most regions, prevailing seasonal environmental conditions impose restrictions on both availability of plant food and ability for continuous growth, development and reproduction throughout the year. Grazing insects have therefore adapted to a seasonal cycle of change in rate of development, alternating between periods of rapid growth and reproduction during favourable conditions, and a period of rest or dormancy during adverse conditions. Such life-cycles have been termed "heterodynamic" (Roberts 1978), and are typical of temperate latitudes where low temperatures during winter are the limiting factor, but may also occur in response to the alternation of wet and dry seasons in the tropics.

In North America the larch sawfly, *Pristiphora erichsonii*, overwinters as a fully developed larva in a cocoon in moss and litter beneath the host trees, while the jack-pine sawfly, *Neodiprion banksianae* overwinters as eggs in the pine needles (Graham and Knight 1965). Loi (1970) reported that a chrysomelid beetle defoliator of poplar, *Melasoma populi* L., overwinters as

adult beetles during the winter in Italy, while Lindquist and Davis (1971) reported a similar finding for the chrysomelid birch leaf beetle, *Phratora hudsonia* Brown, in Canada. Garthwaite (1938), working in a tropical climate, found that the chrysomelid beetle, *Calopepla leayana* Latreille, a defoliator of the hardwood *Gmelina arborea* Roxb.,in northern Burma, undergoes dormancy as the adult beetle during the dry season.

### 3.1.2. Defensive strategies

Defensive adaptations for protection against predation, parasitization and diurnal climatic extremes are of particular significance to the immature stages of grazing insects, due to the large proportion of time spent feeding exposed on plant foliage.

In plant species where the flat leaf lamina is directed towards the sunlight, larvae were often secretive in their feeding habits, feeding on the undersurface of the foliage as in the case of *Chrysomela crotchi* and *Calopepla leayana* (Smereka 1965; Garthwaite 1938). Carne (1962) reported noctural feeding of Australian pergid sawflies.

Many grazing larvae show a strong defensive reaction when disturbed. Pergid sawfly larvae raise their abdomens and regurgitate an oily fluid from their mouths which contains essential oils of the genus *Eucalyptus* on which they feed (Morrow *et al.* 1976). Larvae of some chrysomelid leaf beetle species are equipped with a toxic defensive secretion which is secreted by eversible abdominal glands when the larvae are disturbed. Moore (1967) identified hydrogen cyanide and benzaldehyde from the defensive secretions of the tribe Paropsini,

while Wallace and Blum (1969) identified salicylaldehyde from *Chrysomela scripta* F. Both secretions were toxic to small ants and both authors remarked on the aposematic markings of the larvae and reported a strong defensive reaction associated with secretion of the fluid.

### 3.1.3. Colonial behaviour

The gregarious, or colonial, group-feeding and resting behaviour of a number of grazing insects has been studied in some detail (Ghent 1960; Knerer and Atwood 1973; Carne 1962, 1966, 1969), although the advantages conferred to the species which have adopted this behaviour have not been fully resolved. Ghent (1960) in a study of this type of behaviour in larvae of the jack-pine sawfly, *Neodiprion pratti banksianae* Roh., considered the major advantage conferred was that a number of larvae were able to take advantage of an incision made through a tough needle cuticle by one larva. With larvae of the *Eucalyptus*-defoliating sawfly, *Perga affinis affinis* Kirby, Carne (1966) also found a relatively lower mortality among larvae in large groups feeding on marginally favourable foliage. Carne concluded that this type of 'sub-social' behaviour may permit the species showing it to persist in marginal environments, where as solitary insects, they could not survive:

> "It may be significant that many of the most serious and most widely-distributed forest insect pests are gregarious during those growth stages most susceptible to environmental stresses." (Carne *loc. cit.*)

Protection from predators and parasites has been advanced as an explanation of gregarious larval behaviour. Tostowaryk (1971) found that among diprionid sawfly communities, insect predation and parasitism was greater at the peripheries of the colonies than in their centres, and that larger colonies received relatively less attack due to more effective defensive reactions. Matthews (1976) considered defence against avian predators to be the ultimate explanation. Gregarious species often showed strong aposematic coloration and defensive reactions which were further reinforced when displayed by a group rather than by an individual, while solitary species were often cryptically coloured and secretive in their habit.

Knerer and Atwood (1973) reported that among two congeneric species of sawfly that feed on spruce, *Pikonema alaskensis* (Roh.), a gregarious species was common and could kill trees, while *P. dimmockii* (Cresson), a solitary species, was rare and well dispersed.

Gregarious, group-aggregative behaviour therefore appears to be a valuable adaptive tool in the particular population strategy employed by some grazing insects.

## 3.2. Co-existence and competition

### 3.2.1. Competitive displacement principle

"It is only by adaptation to different sorts of food, or modes of food getting, that more than one species can occupy the same locality. Two species of approximately the same food habits are not likely to remain long evenly balanced in numbers in the same region. One will crowd out the other." This statement by

Grinnell (1904) is considered by De Bach (1966) to be the first expression of the "competitive displacement principle" which is pertinent to many closely related species of grazing insects. The large amount of literature on this topic of the possibility of co-existence of species based both on laboratory experiments and field studies is well reviewed by De Bach (1966) and Price (1975).

### 3.2.2. Niche differentiation

A number of recent field investigations have focussed attention on niche differentiation among closely related phytophagous insects which appear to co-exist in a particular locality. Hicks and Tahvanainen (1974) found that the co-existence of six closely related crucifer feeding chrysomelid flea beetles was due to distinctive host-plant preferences and micro-habitat differences. The highest competitive interaction occurred between *Phyllotreta striolata*, a generalized species with respect to host-plant and micro-habitat, and *P. cruciferae*, which fed on *Brassica nigra* in open, sunny fields. However, Tahvanainen (1972) showed that these two species occurred on different leaf surfaces on *Brassica*. Similarly, in a study of two monophagous species of sawfly both feeding on jack-pine, All and Benjamin (1975) found a temporal differentiation with respect to feeding preferences. Foliage was acceptable to *Neodiprion swainei* Middleton earlier in the season than to *N. rugifrons* Middleton.

Ross (1957) reported the co-existence of several species of leaf hoppers of the genus *Erythroneura* on sycamore trees in Illinois. In a study of competition among the eight species involved, McClure and Price (1975) found certain species pairs were less adversely affected by high density than others, which

suggested slight differences between these species in the manner in which they utilized limited resources. However, these authors considered that slightly reduced levels of competitive interaction were insufficient to explain co-existence by niche segregation. Co-existence in the sycamore leaf-feeding guild was possibly explained by the relative rates of dispersal and extinction among competing species.

### 3.2.3. Hybridization

Hybridization between closely related species which appear to co-exist seems rare. Ross (1957) looked for hybrid forms among *Erythroneura* species with morphologically similar male genitalia, but found none. Smith (1954) found no evidence of hybridization between spruce and jack-pine budworms (*Choristoneura fumiferana* (Clem) and *C. pinus* Free respectively) in a partial breakdown of temporal and niche isolation between these species.

Conversely, niche of different forms of polymorphic species complexes appears to be widely separated such that co-existence never occurs, as shown by Knerer and Atwood (1973) for several polymorphic sawfly complexes, and by Brown (1956) for the *Chrysomela interrupta* F. complex.

### 3.2.4. Co-existence due to effects of predators and parasites

Paine (1966) and Slatkin (1974) have suggested that species may be permitted to co-exist due to the effects of predators and parasites. This concept was employed to explain vegetational diversity by Harper (1969), who suggested that parasitic and predatory activity on a plant species could reduce its density to a level where further species could establish themselves in

the same niche. In Australia, species of *Eucalyptus* tend to form stable associations of two to six species (Pryor 1959). A model of plant competition mediated by host-specific parasites has been developed by Chilvers and Brittain (1972). Investigations by Burdon and Chilvers (1974a, b) have further supported the hypothesis that phytophagous insects, together with pathogenic fungi, play an important role in the maintenance of stable associations between co-dominant species of *Eucalyptus*.

### 3.3. Host specificity

Ehrlich and Raven (1964) suggested that the plant-herbivore interface may be the major zone of interaction responsible for generating terrestrial organic diversity. They considered that the origins of organic diversity, the reciprocal selective responses between closely linked organisms, have been vastly under-rated.

Reviews of host selection and preference by phytophagous insects were provided by Dethier (1954), who discussed the evolution of specificity, and Thorsteine (1960) who outlined the steps involved in food-plant recognition.

#### 3.3.1. Plant secondary compounds and the evolution of host preferences

The mechanism of acceptance of or resistance to feeding insects by plants remained obscure until Fraenkel (1959, 1969) proposed that the large range of "secondary" compounds produced by plants (essential oils, alkaloids, glycosides, tannins, etc.) provided the stimulus to which the insect responded. The "raison d'être" for this class of compounds in plants had hitherto been inadequately explained.

In the long course of evolution of plants and phytophagous insects, plants developed protection from insect feeding by the evolution of repellent chemicals. Some of these repellents were overcome by the evolution of detoxification pathways in some of the species of insect enemies which, in turn, were able to use these compounds as specific sensory cues in the identification of their host plants. Fraenkel suggested that all phytophagous insects had essentially similar nutritional requirements which were adequately provided by most plants. The frequently observed monophagy or oligophagy among phytophagous insects was therefore the result of a long evolutionary chemical struggle between insects and their host plants. Beck (1965) suggested that all plants were not nutritionally adequate for all phytophagous insects, and that feeding stimulants were frequently nutritionally important substances.

The chemical basis of host selection of the chrysomelid Colorado potato beetle, *Leptinotarsa decemlineata* Say, a naturally oligophagous insect occurring on the plant family Solanaceae, has been reviewed by Hsiao (1969) and Chapman (1974). Hsiao and Fraenkel (1968a) showed that a greater range of solanaceous and non-solanaceous plants supported larval development than were attractive for oviposition. However, one species, *Solanum nigrum*, which was highly attractive for oviposition, was never grazed by adults or larvae. These authors considered that the selection of an oviposition site was the first and primary step in host selection by *L. decemlineata*, due to the restricted mobility of the larvae. They found evidence to suggest that oviposition stimuli (both positive and negative) were chemical and not physical

in nature. Visser and Nielsen (1977) demonstrated that unfed, newly emerged females and unfed post-diapause beetles were attracted by the volatiles of several solanaceous and one non-solanaceous species. They concluded that olfactory orientation would mainly lead *L. decemlineata* adults towards solanaceous species.

Feeding responses of *L. decemlineata* larvae have been found to be regulated by a number of chemical stimulants (sugars, amino acids, phospholipids and chlorogenic acid) and deterrents (a number of alkaloids, including demissine and tomatine) (Hsiao 1969; Chapman 1974). Hsiao and Fraenkel (1968b) found evidence that chlorogenic acid and possibly an unidentified phenolic flavenoid acted as specific stimuli. When larvae were fed on artificial diets and acceptable, non-solanaceous hosts, an adaption period involving starvation and test-biting occurred before normal feeding could proceed. However, once normal feeding commenced it was maintained, indicating the important ability of the larvae to adapt to feeding without specific sign stimuli. The general stimulants (sugars, amino acids and phospholipids) were all nutritionally important factors. Grison (1957, 1958) (quoted by Hsiao 1969) showed that the amount of phospholipids in the food plants influenced the fecundity of potato beetles. Inferior larval development and reduced oviposition have been recorded on a number of solanaceous and non-solanaceous non-hosts of *L. decemlineata*, indicating lack of nutritional adequacy of these plants (Hsiao 1969). Gregoire (1978) showed that discrimination between *Salix* and *Populus* by the chrysomelid *Phyllodecta laticollis* Suff. was due to specific phagostimulants

which were responsible for the choice of *Populus* by the insect. Foliage of *Salix* did not show evidence of any physical or chemical deterrents.

Recently, Hsiao (1978) found evidence for four distinct, geographically isolated host adapted populations of *L. decemlineata* in North America. He considered this finding implied that the formation of host races or biotypes among oligophagous insects must be preceded initially by geographical isolation of the preferred and non-preferred hosts, so as to allow sufficient time for the insect population to develop adaptation to the less preferred hosts. This was a radically different mechanism to that found with some polyphagous species, in which host race or biotype formation occurs sympatrically without any evidence of geographic isolation.

When Steven (1973) attempted to feed larvae of *Paropsis charybdis* Stål. on a range of non-eucalypt host foliages, none survived. The *P. charybdis* larvae, naturally restricted to feeding on eucalypts, had been fed foliage of the preferred host, *E. globulus* Labill., prior to testing. Foliage of two non-hosts, *Photinia glabra* (Rosaceae) and *Pittosporum tenuifolium* (Pittosporaceae) were readily eaten, but appeared toxic to the larvae. Within the genus *Eucalyptus*, Styles (1970) reported that foliage of *E. fastigata* Deane and Maiden was also toxic to *P. charybdis* larvae.

### 3.3.2. Plant apparency

Feeny (1976) has developed the concept of "plant-apparency" in relation to the chemical defence of plants. Recent research on herbivore-plant association suggested that chemical defences of

plants may vary as a function of their distribution, abundance, and place in ecological succession. As a result of research on patterns of interaction between herbivorous insects and oak trees, *Quercus robur* L., and various Cruciferae, Feeny suggested that there were major differences between the chemical defences of these two groups of plants. Oaks, which were "apparent" to their insect enemies, due to their long existence in ecological time, had relatively high levels of defensive tannin compounds in their foliage which were generally unpalatable to a wide range of insects at high concentrations. In contrast, crucifers, which were "unapparent" to enemies, due to their ephemeral existence early in ecological successions, had relatively low levels of defensive glucosinolate compounds in their foliage. These compounds were highly toxic to a wide range of insects, but were easily detoxified by a few species. These species were then able to use these highly specific compounds as host-plant attractants. Feeny considered that these two types of defence strategy represented the two ends of a continuous spectrum of chemical defence which varied in time and space as a function of their varying component apparencies to different arrays of enemies, and as a function of varying component importance to plant fitness.

A number of authors have reported variability of resistance of tree foliage to insect attack, depending on its age. Mature foliage of jack-pine, *Pinus banksiana* was more acceptable to larvae of the sawflies *Neodiprion swainei* Middleton, and *N. rugifrons* Middleton than juvenile foliage (All and Benjamin 1975a). All and Benjamin (1975b) found that *N. swainei* and *N. rugifrons* larvae were inhibited in their feeding by extracts of juvenile foliage.

The inhibitor(s), though present in mature foliage, was in lower concentration, and *N. rugifrons* was more sensitive to it than *N. swainei*. *N. swainei* was therefore often displaced to more juvenile foliage by *N. rugifrons*. Other sawfly species were slightly deterred, or not at all affected by juvenile foliage extracts.

On the common oak, *Quercus robur*, Feeny (1976) divided the lepidopteran defoliators into two categories on the basis of their larval phenology. An early-feeding group attacking the relatively nutritious young leaves in the spring included some very abundant species which periodically caused extensive defoliation. A late-feeding group was characterized by slow growth and relative rarity. Feeny (1970) found that the slow growth of most lepidopteran caterpillars on mature oak leaves was due to an increase in leaf toughness accompanied by a reduction in nitrogen and water content as the leaves matured. Drooz (1970, 1971) working with the elm span-worm, *Ennomus subsignarius* (Hubner), found that the juvenile foliage of red oak, *Quercus rubra* L. and pignut hickory, *Carya glabra* (Mill.), promoted significantly better larval development and fecundity than mature foliage. When *Crescentia alata* (Bignoneaceae) trees in Costa Rica were hand-defoliated during the middle of the wet season, the crop of new leaves produced was severely attacked and eaten by adult chrysomelid flea beetles (*Oedionychus* sp.) (Rockwood 1974). A similar defoliation was repeated on the resulting crop of new leaves. Rockwood concluded that adult beetles readily ate any new leaves they could find, but did not normally eat mature leaves.

Feeny (*op. cit.*) considered that the tannon content of oak leaves increased as the season progressed. Since polyphenolic

compounds denature proteins, the decline of available nitrogen in leaves was hastened by the increasing tannin content forming relatively indigestible complexes with leaf proteins. This was a generalized action, hence susceptibility to counteradaption by specific detoxification mechanisms in insects would be low.

When Fox and Macauley (1977) investigated the effect of tannins and polyphenols in the leaves of *Eucalyptus* species on the feeding of *Paropsis atomaria* Olivier, they found these secondary compounds had little effect on feeding rates and nitrogen use efficiency of the larvae. The growth of *P. atomaria* larvae was much more closely related to total nitrogen content of the leaves of the thirteen eucalypt species on which they were fed, than to the tannin content of these foliages. Fox and Macauley considered that the alkaline gut of *P. atomaria* larvae (pH 8.5) could have been responsible for preventing binding of leaf proteins by tannins.

Bernays (1978) has sounded a note of caution in the interpretation of the role of tannins in plants. She considered that while plants could benefit from the presence of tannins in reducing herbivore impact, insects were adapted to cope with such chemicals at an early stage in evolution. The "raison d'être" for the presence of tannins in plants therefore was primarily unrelated to defence against insects. However, in particular situations, they could have an added value in a defensive role.

### 3.3.3. Host specificity among insects which graze on *Eucalyptus*

The genus *Eucalyptus*, which dominates Australian forests and woodlands, has been considered highly susceptible to attack by phytophagous insects (Pryor 1952, 1976; Jacobs 1955; Springett 1978). Morrow (1977) suggested that it would be reasonable to

predict that *Eucalyptus*-grazing insects would be generalized feeders, because most species in the family Myrtaceae (to which *Eucalyptus* belongs) had very similar categories of secondary compounds. These consisted of essential oils and polyphenols (tannins), but not alkaloids, mustard oil glucosides, quinones, or glycosides.

The very large number of species of *Eucalyptus* have been classified in a number of ways, the most recent of which is that of Pryor and Johnston (1971) who subdivided the genus into seven sub-genera. These sub-genera were each divided into a number of sections which, in turn, were divided into series. The classification is based on a wide range of characters and attempts to group species on the basis of inferred phylogeny.

The literature on host-preferences among *Eucalyptus*-feeding insects falls into two main categories, *viz.*: (1) "community surveys", in which all the insects occurring on an association of eucalypts are listed and ascribed preferences according to occurrence, and (2) studies in which the performance of an insect species on a range of hosts is assessed.

3.3.3.1. Community surveys

Burdon and Chilvers (1974a) and Morrow (1977) both made detailed surveys in SE Australia of insects attacking eucalypts which grew in associations including representatives of the sub-genera *Monocalyptus* and *Symphyomyrtus*. Burdon and Chilvers found that of seventeen species of insects, including both grazers and sap-suckers, four species showed a preference for *Symphyomyrtus*, and three species showed a preference for *Monocalyptus*. In an

association of two *Monocalyptus* and one *Symphyomyrtus* species, Morrow found 63 percent of the phytophagous insects (grazers and sap-suckers) collected,attacked only one eucalypt species, 30 percent attacked two species, and 8 percent only,fed on all three species.

3.3.3.2. Individual species studies

Varying degrees of host specificity are reported concerning the grazing insect pests of eucalypts. Among the phasmatids, *Didymuria violescens* was reported (Readshaw 1965) to feed on a range of both *Monocalyptus* and *Symphyomyrtus* species, while *Ctenomorphodies tessulatus* (Gray) was truly polyphagous, feeding on a wide range of species of the genera *Eucalyptus, Syncarpia, Acacia* and *Casuarina* (Hadlington and Hoshke 1959). Morgan and Cobbinah (1977) found that out of 240 species of eucalypts, tested for oviposition suitability for the skeletonizing caterpillar, *Uraba lugens,* 150 species were acceptable. However, larvae were successfully reared to the fourth instar (i.e. with 75% survival) on only seven species. Although *Symphyomyrtus* species appeared to be most preferred for oviposition, successful survival to the fourth instar larval stage occurred on only four *Symphyomyrtus* species, and on three non-*Symphyomyrtus* species. Morgan and Cobbinah also found that caterpillars would readily accept as food some eucalypt species which were constantly avoided for oviposition. Hence larval feeding preferences did not necessarily reflect oviposition preferences.

Females of the sawfly *Perga affinis affinis* were found to oviposit preferentially on foliage of *Symphyomyrtus* species:- *E. blakelyi* Maiden, *E. camaldulensis* Dehn., and *E. melliodora* A. Dunn. by Carne (1965). In a study of the Christmas beetles

*Anoplognathus porosus* and *A. chloropyrus* attacking young *E. grandis* (*Symphyomyrtus*, section Transversaria) grown in plantation, Carne *et al.* (1974) reported that when *E. dunnii* Maiden (*Symphyomyrtus*, section Maidenaria) was included in the plantations, this species was preferentially attacked by *A. chloropyrus*.

Among the paropsids which graze on eucalypts, the host range of *Paropsis charybdis* in New Zealand is the best documented. This species, introduced into New Zealand, is a pest of eucalypts planted in that country. White (1973) recorded the feeding of *P. charybdis* on 59 species of eucalypts, but of these, only six *Symphyomyrtus* species in three sections (Transversaria, Maidenaria, and Adnataria) (*E. deanei* Maid., *E. resinifera* Sm., *E. globulus* Labill., *E. macarthuri* Deane and Maid., *E. viminalis* Labill., and *E. leucoxylon* F. Muell.), were extensively and repeatedly defoliated.

Steven (1973) assessed the performance of larvae of *P. charybdis* in the laboratory on the foliage of eight *Symphyomyrtus* species, seven *Monocalyptus* species and one species of the sub-genus *Corymbia* (*E. ficifolia* F. Muell.). The survival, duration of larval development, and pupal weight of larvae reared on each foliage were measured, and foliage type ranked according to a summation of rankings of foliages for larval performance in each parameter measured. Of the sixteen species of eucalypts tested, two non-*Symphyomyrtus* species (*E. ficifolia* and *E. fastigata*) would not support larval growth. With some species Steven found marked differences in the ability of foliage collected from different localities to support larvae. Foliage of the *Monocalyptus* species *E. obliqua* L'Herit. from one source was ranked second best, while foliage of *E. obliqua* from two other

sources were ranked second worst, and worst, respectively. Mature foliage of the *Symphyomyrtus* species *E. globulus* was ranked third best while juvenile foliage of the same species was ranked fourth worst.

While a general preference of *P. charybdis* in the field for *Symphyomyrtus* species was apparent from observations (White 1973), Steven (1973) found that the five best ranking foliages for *P. charybdis* larvae in laboratory trials included three *Symphyomyrtus* species (*E. camaldulensis* (1), *E. globulus* - mature (3) and *E. perriniana* (4)) and two *Monocalyptus* species (*E. obliqua* (2) and *E. delegatensis* (5)). Steven (*loc. cit.*) concluded that there was little correlation between foliage suitability for *P. charybdis* larval growth and the taxonomic relationships of the species of *Eucalyptus*.

In a study of the closely related *Paropsis atomaria* in its natural habitat in S.E. Australia, Carne (1966) found that the *Symphyomyrtus* species *E. blakelyi*, *E. melliodora* and *E. polyanthemos* Schau., together with the *Monocalyptus* species *E. fastigata* were most commonly attacked. However, in laboratory trials, larvae performed best on *E. macrorhyncа* F. Muell. ex Benth. foliage, a species on which *P. atomaria* females did not oviposit in the field.

Greaves (1966) and Kile (1974) reported that the Tasmanian species, *Chrysophtharta bimaculata* (Olivier), preferred *Monocalyptus* species of the series Obliquae, *E. obliqua*, *E. delegatensis* and *E. regnans*. De Little and Madden (1975) investigated the host preferences of two sympatric species, *C. bimaculata* and *C. agricola* (Chapuis). Foliage of the *Monocalyptus* species *E. delegatensis*,

the species on which *C. bimaculata* was commonly encountered and on which the occurrence of *C. agricola* was rare, was found to be as suitable as a larval food for this latter species, as was the species on which it commonly occurred, *E. dalrympleana* Maid. (*Symphyomyrtus*).

The literature concerning the host preferences and specificity of the paropsids on eucalypts therefore appears to indicate complex relationships in which observed oviposition preferences are not always reflected by palatability of foliage to larvae, and in which variation in palatability within host species may occur.

## 3.4. Efficiency of utilization of food plant

### 3.4.1. Efficiency of conversion of food to body matter

Since phytophagous insects do not thrive equally well on all plants on which they may successfully complete their life cycles, a number of studies have investigated their abilities to utilize food plant material. Waldbauer (1968) and Beck and Reese (1976) have reviewed the methods for evaluating feeding indices. An index commonly used to express the efficiency of conversion of ingested food to body tissue is the ratio of body weight gained to weight of food ingested. When expressed on a dry weight basis, this index is known as the efficiency of conversion index (ECI).

ECI values for a particular insect may vary widely,depending on the host plant being grazed. Soo Hoo and Fraenkel (1966) found a wide range of ECI values when they investigated the performance of fifth instar larvae of the polyphagous Southern army worm, *Prodenia eridania* (Cramer) on a range of food plants. Colorado potato beetle, *Leptinotarsa decemlineata*, when reared on tomato, fed longer, consumed more foliage, and had a lower

survival rate than when reared on potato, its principal host. Latheef and Harcourt (1972) found higher ECI values for potato foliage than for tomato foliage for all larval instars of *L. decemlineata*.

### 3.4.2. Efficiency of conversion of eucalypt foliage

Carne (1962, 1966) calculated ECI's on a fresh weight basis (gross conversion ratios) over all instars of two larval grazers of *Eucalyptus blakelyi* Maid.; the sawfly *Perga affinis affinis*, and the paropsid, *Paropsis atomaria*. Values of 0.242 and 0.200 were calculated for sawfly and paropsid respectively, these values being intermediate among gross conversion ratio values cited in the literature.

Many authors have stressed the importance of individual nutrient elements for effective growth, development and reproduction. White (1978) has proposed that for most animals, the single most important factor limiting their abundance is a relative shortage of nitrogenous food for the young, growing individuals.

In a study of the effect of differing nitrogen levels of cruciferous food plants on caterpillars of the cabbage white butterfly, *Pieris rapae* L., Slansky and Feeny (1977) correlated an increase in ECI of fifth instar larvae with an increase in nitrogen level of food. Fox and Macauley (1977) found a similar correlation with fourth instar *Paropsis atomaria* larvae, but both ECI values and nitrogen levels were lower than those recorded by Slansky and Feeny. Fox and Macauley considered that eucalypt leaves represented a food source of low nutritive value, particularly with respect to nitrogen, for their insect grazers. Hence, in adapting to grazing on eucalypt foliage, insects have

adapted to a food source of relatively lower nutritive value than average, and are thus constrained to ingest greater quantities of food material.

### 3.5. r and K strategies

The concept of r and K selection formulated by Macarthur and Wilson (1967) has considerable application in evaluating ecological strategies employed by animal and plant species (Pianka 1970, 1972; Gadgil and Solbrig 1972; Southwood *et al.* 1974; Force 1975; Grime 1977).

The terms "r" and "K" were derived from the logistic population equation; r denoting the intrinsic rate of increase of a population, and K denoting the carrying capacity of the environment. r-selected species maximized gross food intake and reproduction rate, while K-selected species maximized efficiency of food usage and replaced themselves with a minimum of offspring. Species which adopted an r-strategy operated where niche-hypervolume was frequently empty, and the premium was on the ability to exploit this opportunity rapidly. However, K-strategists maximized their share of a fully packed niche-hypervolume. Hence K-species populations did not fluctuate far from their equilibrium point, while r-species populations were liable to considerable fluctuations (Southwood *et al.* 1974). Thus the stability of the habitat was important in influencing the ecological strategy of the species.

While it has been suggested that the tropics (more stable habitat) favour K-strategists, and that temperate climates (less stable habitat) favour r-strategists, and that vertebrates and trees are good examples of K-strategists while many insects and ephemeral plants are good examples of r-strategists, Pianka (1970)

and Gadgil and Solbrig (1972) have stressed that these two types of selection represent two ends of a continuous spectrum:

> "The concept of r- and K-strategists is meaningful only on a comparative basis, there being no absolute criterion to determine whether an organism should be classed as an r- or K-strategist."

Greenslade (1972) proposed three phases in the evolutionary radiation of the tropical staphylinid genus *Priochirus*, species of which inhabit rotting logs. In the initial phase, r-selection for productivity among unspecialized forms predominated in disturbed lowland rainforest, and at its margins. Large populations enabled range extension and this provided opportunities for speciation through geographical isolation. The next phase of radiation was one of K-selection for efficiency as the intensity of species interaction steered new species to stages of log decay least effectively occupied by existing fauna. This entailed a shift of habitat towards later stages of log decomposition, and to logs in montane forest. In the final stages of radiation, in montane habitats, Greenslade recognized a "beyond K" type of selection in which species became highly adapted to specialized habitats. In their adaptation to extreme conditions, "beyond K" species were protected from competition with other forms, but also became unfitted to recolonize sites and stages of log decay from which major cycles of range expansion usually started.

It has been suggested that species which successfully establish in new geographical regions are highly r-selected. Southwood *et al.* (1974) has quoted as an example, Colorado potato beetle, *Leptinotarsa decemlineata*, which colonized an entire continent from the introduction of a few individuals.

The r and K selection concept has been considered too simplistic a framework on which to base explanation of life history and ecological strategy. Hairston *et al.* (1970) noted that selection could not act directly on the instantaneous rate of increase (r) of a population, but instead acted on its components, the birth and/or death rate. Wilbur *et al.* (1974) considered that evolutionary theory had not yet determined the necessary and sufficient environmental factors that could be used to explain the observed diversity of life history patterns. The r and K selection concept was inadequate to explain life histories of many organisms due to the fact that they showed both r and K characteristics. Pianka (1972) claimed that although the terms "r" and "K" might be unfortunate to the extent that they invoked the over-worked logistic population equation, the concepts accompanying them were independent of that equation and were both clear, and extremely useful in modern population biology.

## 4. Life History: *Chrysophtharta bimaculata* compared and contrasted with other paropsid and non-paropsid chrysomelid species

The most universally studied chrysomelid is undoubtedly the Colorado potato beetle, *Leptinotarsa decemlineata* Say, of the subfamily Chrysomelinae and tribe Chrysomelini, which originally fed on natural Solanaceae in Colorado, but has spread throughout northern America on potato, *Solanum tuberosum*, and has become established in Europe on that host (Johnson 1969). The tribes Paropsini and Dicranosternini also belong to the Chrysomelinae, and the only detailed published studies of paropsid life histories are of *Paropsis atomaria* (Carne 1966) and *Chrysophtharta bimaculata* (Greaves 1966). Life histories of other Chrysomelinae which have been studied in detail are *Phytodecta olivacea* (Forster) which attacks broom, *Sarothamnus scoparius* L., in the British Isles and N.W. Europe (Waloff and Richards 1957); *Chrysomela crotchi* Brown, a defoliator of trembling aspen, *Populus tremuloides* Michx., in Canada (Smereka 1965); and *Phratora hudsonia* Brown, a defoliator of birch, *Betula* spp., in Canada (Lindquist and Davis 1971).

### 4.1. Life cycle

Greaves (1966) gave a detailed account of the life cycle of *C. bimaculata* on *Eucalyptus regnans* regrowth in the Florentine Valley in Southern Tasmania. Adult beetles hibernate under bark on the trunks of trees and in cracks in the wood of dead trees. Adults leave their overwintering sites in spring and congregate on foliage of young regrowth trees. They actively fly and feed on warm, sunny days, but in cool, or windy weather, they seek

shelter among ground litter. Oviposition takes place in hot, sunny weather in late spring, or early summer. Eggs are laid in rafts on new foliage, and have an incubation period of nine to eleven days. Following eclosion, larvae feed first on the choria of their eggs, and then commence feeding in a group on the leaf margin on which the egg raft is deposited. As larvae grow, they migrate on to older and tougher leaves to feed. There are four larval instars, each lasting from five to six days, and as maturity is approached, feeding groups tend to break up. On completion of growth, larvae fall to the ground, where they burrow into the litter for a short distance and form small prepupal cells. The pupal stage follows five to nine days later, and lasts a further twelve to fifteen days. The new adults emerging from pupation sites congregate in the tree foliage where they feed and oviposit. This results in a second generation, which goes through all the stages mentioned, and adults in this second generation emerge in autumn. Second generation adults feed, but do not mate or oviposit. They accumulate fat body and, as winter approaches, move into overwintering sites. Thus only every second generation of adults overwinters.

Bivoltine life cycles have also been reported for *P. atomaria* in the Australian Capital Territory (Carne 1966), *Chrysophtharta variicollis* (Chapuis) in the A.C.T. (P.B. Carne, unpublished information) and for *P. charybdis* in New Zealand (Styles 1970). In the warmer climate of northern coastal New South Wales, both *P. atomaria* and *C. cloelia* passed through at least three, and possibly four generations per annum (Carne *op. cit.*). In the cool, temperate regions of the northern hemisphere, Chrysomelinae are chiefly univoltine (Waloff and Richards 1957; Smereka 1965;

Lindquist and Davis 1971). *L. decemlineata* is uni- to trivoltine throughout its wide distribution range in north America and Europe.(Metcalf and Flint 1939; Harcourt 1963; Kovtun 1966; Krasnovskaya and Vorotyntseva 1967). Carne(1966) noted considerable variation in the phenology of *P. atomaria* on the same trees in different seasons, and between different sites in the same season. He concluded that this was a function both of the phenology of the host trees, and of the prevailing weather conditions.

4.2. Dispersal

Although there is no published account of migration and dispersal of *C. bimaculata* adults, large numbers of beetles have been observed in flight on a number of occasions (D. de Boer, J.L. Madden, *pers. comm.*). Carne (1966) made a study of the dispersal of *P. atomaria*. White (1973) and Johnson (1969) have reviewed the establishment and spread of *P. charybdis* and *L. decemlineata*, respectively, both of which species have considerably expanded their natural range as a result of man's activities.

In studying the dispersal of *P. atomaria*, Carne (*op. cit.*) concluded that the species was highly sedentary, although the adults flew readily and vigorously and appeared capable of dispersing over substantial distances. This seemingly contradictory conclusion was based on the observation that in plantation study sites, the patterns of relative abundance of adults in early summer, on rows of different eucalypts, remained more or less constant from year to year. When mature adults were liberated in sites where there were apparently favourable hosts free of *P. atomaria*, egg batches were only found close to the tree of release.

*P. charybdis*, a comparatively rare species in Australia (Styles 1970) was first reported in the Canterbury district of New Zealand in 1916. By 1938 it had spread throughout the northern and eastern regions of the South Island, but it did not reach Westland until the 1960's. The first recorded establishment in the North Island was on the S.W. coast in 1956, and in less than ten years it had spread throughout the entire island (White 1973).

*L. decemlineata* started to spread when settlers brought the potato, *Solanum tuberosum*, to its limited natural range in Colorado about 1845-50. Thus a wide expanse of host-free country isolating the eastward spready of the beetle was bridged, and the beetle spread across North America, reaching Quebec by 1874. It first became established in Europe near Bordeaux in 1922 and took 35-40 years to become established over a range of about 2,000 km (Johnson 1969).

Although *L. decemlineata* was considered a sluggish flier, capable of flying from 13-14 minutes in a single flight, and at a speed of no more than 8 km $hr^{-1}$ (Feyland 1930), beetles have been reported to travel long distances on strong winds (Johnson 1969). White (1973) considered that the successful colonization of the North Island of New Zealand by *P. charybdis* resulted from many beetles being blown across Cook Strait from Nelson after they became abundant there in the early 1950's. Adult *P. charybdis* and *L. decemlineata* have both been recorded on mountains at up to 2,000 m (White 1973; Wegorek 1959).

Both species have been observed flying in warm, sunny weather in late spring prior to oviposition (White 1973; Johnson 1969) and in spite of the apparent inability of the beetles to make unbroken, long distance flights, their ready ability to disperse is unequivocal.

4.3. Diapause

The phenomenon of diapause has been reported in two paropsid species: *P. atomaria* (Carne 1966) and *C. bimaculata* (Davies 1966). Mansingh (1971) has classified insect dormancies into three types:

1. hibernation, due to temperatures lower than optimum;

2. aestivation, due to temperatures higher than optimum;

and, 3. a thermopause, due to factors other than temperature. Diapause is the most extreme form of dormancy in any of these physiological conditions, as opposed to the lesser conditions of quiescence and oligopause. Thus diapause is the most highly evolved system of dormancy for overcoming cyclic, long-term and extreme environmental conditions, is induced well before the adversity, and is maintained for some time irrespective of the environment (Mansingh *loc. cit.*). The usual method of perception of on-coming seasonal change is through a regular seasonal rhythm such as photoperiod (Lees 1956; de Wilde 1962; Danilevskii 1965; Beck 1968).

In the majority of species, including *L. decemlineata*, diapause was induced by short day-lengths and suppressed by long day-lengths or continuous illumination (Lees *loc. cit.*). This was also the case with *P. atomaria* (Carne 1966) and *C. bimaculata* (Davies 1966). Goryshin (1958) found that the threshold photophase of *L. decemlineata* was dependent on temperature. The threshold photophase varied from greater than 18 hours for beetles maintained at 18°C, to 14 hours 30 minutes for beetles maintained at 30°C.

In the Chrysomelinae, the adult stage was the stage most strongly sensitive to photoperiod induction of diapause (Carne *loc. cit.*; Davies *loc. cit.*; Danilevskii 1965). In general, beetles emerging from pupation late in the season accumulated

fat-body prior to diapause instead of attaining sexual maturity. However, some Chrysomelinae in the northern hemisphere survive for more than one season, and regression of ovaries was observed in females prior to the second diapause (de Wilde 1953; Waloff and Richards 1957; Smereka 1965). Davies (1966) induced *C. bimaculata* to diapause in the laboratory after reproductive activity. Although the adult stage was the most strongly sensitive to photoperiod, de Wilde *et al.* (1959) and Hodek (1971) found that photoperiods experienced by *L. decemlineata* larvae could influence the induction of adult diapause. Reports on the effect of food quality on diapause of *L. decemlineata* are conflicting. Larczenko (1957) reported having detected a correlation between the incidence of diapause and the lipid/protein ratio of the food; however, Wegorek (1960) was unable to confirm these results. De Wilde (1962) considered food to be the second most important factor in diapause of *L. decemlineata*, as both senescent leaves and shortage of food could induce diapause. Beck (1968) was only prepared to state that "there are a number of observations that lend at least limited credence to the hypothesis that diapause incidence may be slightly influenced by nutritional effects".

Danilevskii (1965) drew attention to the fact that although diapause was often described as a state of physiological rest, it was not, however, a completely inactive state. Physiological processes were continuously taking place which led to the reactivation of the insect. One of the most characteristic features of diapause was the unique dependence of reactivation on temperature. Carne (1966) considered that diapause was terminated in *P. atomaria* as a result of higher temperatures

bringing about the depletion of a metabolite, and that photoperiod played no part in this process. Davies (1966) suggested that termination of diapause in *C. bimaculata* was a temperature modified photoperiodic response. However, de Wilde *et al.* (1959) considered that diapause in young, adult *L. decemlineata* could be terminated by exposing the insects to several days of long-day photoperiods.

Greaves (1966) made the observation that *C. bimaculata* adults underwent a distinct colour change. Actively feeding and reproducing beetles were a pale green colour while hibernating beetles were a dark brown colour. Davies (1966) considered this colour change to be related to diapause status in *C. bimaculata*, the ultimate criterion of which was taken as the presence of obstructive faecal material in the terminal portion of the alimentary system.

4.4. Reproductive biology, egg potential and oviposition behaviour

Engelmann (1970) observed that a ratio of 1:1 between male and female individuals in a population was common among insects. This ratio was accomplished by both major sex-determining mechanisms, balance between male and female sex determiners and epistatic sex determination. Among Chrysomelinae, Waloff and Richards (1957) found approximately equal numbers of males and females of *Phytodecta olivacea* emerging over the whole season, with females often present in marginally greater numbers than males. However, the sex ratio was found to vary markedly in time throughout each season, males being far more abundant in spring, and females being in greater abundance in autumn. Carne (1966) took weekly samples of 100 adults of *P. atomaria* by sweeping foliage, throughout the season, and found the mean percentage of females in 64 samples to be 55.7 ± 1.1%. He found

no seasonal trend and attributed the slight preponderance of females to sampling error, the females being, on average, slightly heavier than the males. Styles (1970) reported a sex ratio in *P. charybdis*, in New Zealand, of males to females of between 1:1 and 1:2.

Insect reproduction has been reviewed by Engelmann (1970) and de Wilde and de Loof (1973). The reproductive physiology of *Ph. olivacea* was described by Waloff and Richards (1957) and of *L. decemlineata* by de Wilde *et al.* (1959) and de Wilde and de Boer (1961). Carne (1966) found that in *P. atomaria*, the appearance of food in the gut of adults emerged from overwintering was followed almost immediately by development of the gonads. The most conspicuous change in the male was the increasing pigmentation of the testes. In the female the ovaries, which were initially colourless and slender, enlarged until they occupied most of the abdominal cavity. The oocytes in each ovariole ripened successively, becoming opaque and pale yellow. The ovarial calyces acquired a pink colour which darkened progressively as each batch of eggs was laid. When a batch of eggs was laid, each ovariole contributed a single matured oocyte. Davies (1966) studied ovary maturation in *C. bimaculata* under laboratory conditions of 25 $^{o}$C, 16 hours photophase. For the first three days after emerging from pupation, ovaries did not develop. Between days four and six differentiation occurred, and on day seven oocytes were in an advanced state of yolk deposition. On day eight, the chorion was forming around eggs, and on day nine oviposition occurred. Waloff and Richards (1957) found that with *P. olivacea*, in females surviving to over-winter for the second

time, the ovaries regressed until the oocytes were resorbed. However, the reproductive organs of females with regressed ovaries remained larger than those in the immature beetles, hibernating for the first time. Mercer and King (1976) proposed an ovarian development ranking system for use in the description of seasonal ovarian development in the scarab beetle *Heteronychus arator* (F.).

A tendency towards viviparity has been noted in several genera of the Chrysomelidae (Hagan 1951). Although there is no record of this tendency among the paropsids, Waloff and Richards (1957) mentioned the occurrence of viviparity, and ovoviviparity, in which the chorion ruptured shortly after oviposition, in the genus *Phytodecta*. Ovoviviparity was also shown by *Chrysomela varians* (Rathfeldt 1924).

A variable range of potential fecundities for Chrysomelinae is reported in the literature. Latheef and Harcourt (1972) found that females of *L. decemlineata* reared from larvae on potato foliage lived for 75 to 100 days and laid an average of 714 eggs per female. De Wilde and de Boer (1961) reported 1,243 eggs per female to be a productivity of normal beetles under Dutch summer conditions, and Kowalska (1969) reported that female beetles in Poland could lay up to 2,000 eggs each in a season. One-year-old females of *Chrysomela crotchi* had an average fecundity of 132.5 eggs/female while in two-year-old females the average fecundity was 198 eggs/female (Smereka 1965). Waloff and Richards (1957) found that the average fecundity of *Ph. olivacea* females varied from 251 to 320 eggs/female over three successive seasons. Among Paropsini, Styles (1970) reported that female *P. charybdis* were capable of laying from 1,500-2,000 eggs under laboratory conditions over a period of

two to three months. Carne (1966) found that with *P. atomaria*, reproductive capacity was related to the size of females. Size affected the number of eggs per batch, not the number of batches which a female laid. Carne (*loc. cit.*) estimated the potential reproductive capacity of *P. atomaria* to be about 640 eggs/female under favourable conditions. The effect of temperature on egg potential in *C. bimaculata* was investigated by Davies (1966) and Greaves (1966) who found a general increase in numbers of eggs laid per female at higher temperatures. Total number of eggs laid per female was variable ranging from 377 for female maintained at 12°C to 1,311 for a female maintained at 25°C (Davies 1966). Egg potentials of *P. charybdis*, *P. atomaria* and *C. bimaculata* therefore appear to be comparable to those of *L. decemlineata*. Greaves (1966) found infertility of field deposited eggs of *C. bimaculata* to be an infrequent occurrence.

In a study of the effect of field temperature on the timing and quantity of oviposition of *C. bimaculata*, Greaves (1966) found that a dramatic increase of oviposition was stimulated as a result of an exceptionally hot day on which the maximum temperature was 35°C. At one study site where eucalypt shoots were being examined every two to three days for the presence of egg batches, the percentage of the shoots bearing egg batches rose from 48 to 90 following the hot day, while at another site the increase was from 0 to 60 percent. Carne (1966) demonstrated the effect of suitability of foliage on oviposition in *P. atomaria* by selecting two series of trees matched for size and foliage condition. On one set of trees, egg batches were removed before hatching, so that the trees were not defoliated by hatching larvae. The other (control) set of trees was left

undisturbed. While the rate of oviposition of the control trees peaked at 20 batches/day in mid-December, the oviposition rate on the experimental trees reached 50 batches/day in late January. The oviposition curve on the control trees was bimodal due to the production of a second flush of attractive foliage by these trees after defoliation by the first generation larvae. This bimodality of oviposition curve was not observed on the experimental trees.

4.5. Immature development

Waloff and Richards(1957), in a study of the effect of temperature on the development of immature stages of *Ph. olivacea*, fitted Davidson's (1944) formula to the rates of development of eggs, larval stages, and pupae at different constant temperatures. Carne (1966) plotted duration of stage against temperature for the stages of *P. atomaria*, and Greaves (1966) measured the incubation periods of eggs, larvae and pupae of *C. bimaculata*. While minimum developmental time of *P. atomaria* larvae occurred between 22°C and 25°C, *C. bimaculata* larvae developed fastest at 27°C. Carne (1966) found that at 24°C, or at lower temperatures, the weights attained by larvae of *P. atomaria* did not differ significantly. However, very few larvae survived to pupate at 29°C and pupal weights were significantly below normal. Although Greaves (1966) did not note any deleterious effects due to high temperatures on field populations of *C. bimaculata* larvae, Carne (1966) recorded cessation of feeding and dropping from foliage of *P. atomaria* larvae during several heat waves, when the temperatures exceeded 24°C for more than 8 hours on four to five successive days. On succulent, young foliage, mortality rates of up to 40% were recorded in feeding colonies, while mortality rates as high as 80% were recorded on older leaves. Carne considered

that the water balance of feeding *P. atomaria* larvae was precariously maintained at high temperatures. Non-feeding stages of *P. atomaria* appeared to be far better protected against high temperatures, and no increased mortality was recorded during periods of prolonged high temperatures.

About 10% of the total food consumed by both *C. bimaculata* and *L. decemlineata* larvae was consumed during the first two instars (Greaves 1966; Chlodny 1967). *C. bimaculata* larvae consumed 65% of their total food in the fourth instar, while *L. decemlineata* larvae consumed about 70%. Carne (1966) found that *P. atomaria* consumed 14% of its total food during the first two instars, and 50% in the fourth instar. *C. bimaculata* larvae feed on current season's foliage of *E. regnans* regrowth (Greaves *op. cit.*). Although there is usually no shortage of food, when larval populations are very dense, the regrowth can be totally stripped of its new foliage before the larvae have completed their development. Under these conditions, the bark of the growing shoots is next consumed, and finally, larvae attempted to feed on the tough, fibrous previous season's foliage. Weakened larvae, even if not dying directly through starvation, can more easily be dislodged from the foliage by wind and rain.

## 5. The ecology of natural enemies and the paropsid predator/parasitoid complex

### 5.1. Predation

Solomon (1949) suggested that total predation was the product of number of prey killed per predator, and the number of predators present. He proposed two terms to describe these two aspects; the functional response, concerning prey consumption, and the numerical response concerning density of predators. A consideration of these factors led Holling (1961, 1965, 1966) to describe several fundamental predator-prey response models, the basic components of which were: the length of time that the predator and prey were exposed to each other, the rate of successful searching, and handling time. Other subsidiary components, such as hunger, inhibition by prey, and learning by predators were also given consideration because of their ability to influence the response model through the basic components. Holling's (1965) model predicted the results of defence mechanisms such as mimicry, crypsis and defensive reaction. Tostowaryk (1972), studied the functional response of the predatory pentatomid, *Podisus modestus* (Dallas) to densities of larvae of two colonial species of jack-pine sawfly, *Neodiprion swainei* and *N. pratti banksianae*. At higher densities of prey (i.e. with larger larval colony size) a different type of response curve of the predator was obtained, indicating that *Neodiprion* spp. were successful in reducing predation pressure by feeding in aggregates, thus producing a more effective defence against predators through the combined defensive reaction of the group.

Hassell (1966) considered the terms "functional" and "numerical" were unsuitable for describing the effects of parasitization or predation on the host or prey population. He suggested that the response of parasites or predators to their host or prey densities should be considered in proportionate terms, i.e. in terms of changes in the percentage parasitization or predation. He proposed the terms behavioural response, and intergeneration relationships, which would make it easier to discern the effects of the enemy population on the numbers of the host population, as well as showing how the behaviour of the enemy is affected by host density, and how, as a consequence of this, the numbers of the enemy are altered.

The coccinellidae are well known predators of other insects (Hagen 1962, Hodek 1967, 1973). Studies by Dixon (1971), Wratten (1973) and Frazer and Gilbert (1976) have shown that the response of coccinellids preying on aphids was complex. In a field study of the effect of predation by *Coccinella trifasciata* on the pea aphid, *Acyrthosiphon pisum* (Harris), Frazer and Gilbert (*loc. cit.*) found an extremely unstable relationship between predator and prey. An empirical formula for predation rate was derived which included predator and prey densities, predator voracity, prey age-distribution, and temperature. Temperature was a most important factor, both in its differential effect on predation rate, and in its effect on population dynamics of the prey. It was therefore an essential component of predator-prey models. Frazer and Gilbert considered that *C. trifasciata* could not be expected to keep *A. pisum* numbers low for any length of time due to the instability of the predator-prey relationship. At high temperatures, however, a significant suppression of the prey population could be expected.

## 5.2. Parasitization

Price (1975b) defined a parasite as an organism which lives in or on another living organism, obtaining from it part, or all, of its organic nutriment, usually having a negative influence on the fitness of its host, and commonly exhibiting some degree of adaptive modification. The term "parasitoid" has been applied to parasites with a free-living adult stage, in recognition of the fact that the free-living adults have a similar effect on the host population as do predators on their prey. Since each host on which an egg is deposited is killed by the parasitic larva, the adult is responsible for killing many hosts just as is the predator (Reuter 1913, *in* Price, *loc. cit.*). Important consequences of the parasitic habit are specialization of the parasite due to the narrowness of its niche, and a non-random effect on host populations (Price *loc. cit.*) Vinson (1975) pointed out that there were many analogies between the parasite - host relationship and the phytophagous insect - host-plant relationship. Just as chemicals played an important role in host-plant selection by phytophagous insects, they were also important in the parasitoid - host relationship. The host-plants of phytophagous insects often provided the first cues in the chain of steps leading the parasitoid to its host.

Most parasitoids occur in two main orders: the Hymenoptera (Ichneumonoidea and Chalcidoidea) and the Diptera (Tachinidae) (Askew 1971). Price (1975c) considered that for parasitoids, a knowledge of selective factors acting on egg production and the results of natural selection were necessary for a full understanding of the co-evolution of host and parasitoid, host and parasitoid

population dynamics,parasitoid community ecology and for the development of a predictive science in biological control using introduced parasitoids. Price (1973a, 1974, 1975c) considered that the major determinants of fecundity in parasitoids were the probability of finding hosts, and the probability of survival following successful parasitization. Ovariole number in the ichneumonid and tachinid parasitoids was linearly correlated with fecundity. The relative probability of host discovery at different stages of development and of survival in hosts once eggs had been deposited could be predicted from host survivorship curves. Probability of discovery declined in a similar manner to host abundance and probability of survival decreased rapidly as earlier stages of the host were attacked due to the fact that parasitoids emerged from the later stages of development of the host. Price (1975c) suggested these changes in relative probability would influence the pattern in fecundity of the parasitoids and demonstrated an inverse relationship between ovariole number of parasitoid and stage of host attacked for both ichneumonids and tachinids.

Hassell and Varley (1969) investigated theories of parasitoid introduction for biological control from the viewpoint of population dynamics. They derived a theory of "parasite quest", based on studies of parasitoid performance in the laboratory and field, which provided a better interpretation than was possible with previous theories. On this basis, they considered the practice of multiple, or successive introductions to be the best approach. There were three main advantages of multiple introductions: (1) there was a greater chance that at least

one species would be established; (2) if more than one was established, this would be likely to be advantageous, and (3) if the environment included different climatic zones, then, by competitive displacement, different beneficial species could become dominant in different areas.

In an interpretation of parasitoid strategy in terms of r and K selection, Price (1975c) suggested those species that attack early host stages could be regarded as r strategists, and those that attack late stages as K strategists. The parasitoid guild of the Swaine jack-pine sawfly, *Neodiprion swainei*, has been studied in detail (Price 1970, 1971, 1972a, b, 1973a, b, 1974; Price and Trip 1972). Evidence was found to support the hypothesis that parasitoid complexes develop in relation to plant succession. Early colonizers had a high fecundity and low competitive ability (more r-selected) while later colonizers had a low fecundity and high competitive ability (more K-selected), and species diversity in the complex tended to increase as succession proceeded. These trends were also detected in a succession of increasing host densities over several years, and in decreasing host abundance within each host generation (Price 1973b). Force (1970, 1972, 1974, 1975) investigated the strategies of the parasitoids of a vastly different type of host, the cecidomyiid gall midge, *Rhopalomyia californica* Felt, and found strong evidence of r and K selection. At one study site much of the host plant material was removed, and at the next time of sampling, the most r-selected parasitoid had increased its degree of parasitization of the host population from 1% to 46% at the expense of the other, more K-selected species (Force 1975). Askew (1975) also identified parasitoids at

each end of the r-K strategy continuum which attacked gall-making Cynipidae on oaks.

Barbosa (1977) investigated the role of r and K strategies in the life history of three tachinid and two hymenopterous parasitoids of the gypsy moth, *Lymantria dispar* (L.). In a consideration of the life history characteristics of reproductive capacity, time of encounter with host, reproductive mode and number of generations, no consistent r-K trend was found among the five parasitoids. However, clear trends were evident within each of the two orders with respect to these characteristics, although there was no clear trend in relation to host density. It has been suggested (Force 1972) that most parasitoids imported for biological control programmes have been K-strategists due to the fact that they would be more numerous in endemic habitats because of their long-standing association with a host at endemic levels. However, K-strategists would not be as likely to make good biological control agents as r-strategists with their high reproductive capacities, etc., which make them pre-adapted to a colonizing situation. Barbosa (1977),however, considered there was insufficient evidence for such reasoning and, supporting Hassell and Varley's (1969) view, summed up the situation:

> "..... at best, if one assumes that the concept of r and k can be incorporated in biological control strategy, it would seem reasonable that multiple introductions of both r and K strategists should be undertaken. This would use to full advantage the capabilities of a variable parasitoid complex in areas with variable environmental influences and potentially variable host populations.

However, either some modification of current theory or elaboration of available data will be required before it will be possible to consistently and definitively categorize parasitoid species as r or K-strategists". (Barbosa *loc. cit.*)

## 5.3. Predators and parasitoids of paropsids

A number of predator and parasitoid species which attack paropsids have been recorded (Cumpston 1939; Davies 1966; Greaves 1966; Styles 1970; Crosskey 1973; Tanton and Khan 1978; H.J. Elliott and D.W. de Little, unpubl. information).

Species of the hymenopterous families Platygasteridae, Scelionidae and Diapriidae (Proctotrupoidea), Pteromalidae and Encyrtidae (Chalcidoidea) have been recorded as egg parasites of *Paropsis atomaria*. The most common species encountered was *Neopolycystus insectifurax* Girault (Pteromalidae:Pteromalinae) (Cumpston 1939; Tanton and Khan 1978). Tanton and Khan found that parasitization of *P. atomaria* eggs varied between 1% and 20% in weekly collections, but there was no clear seasonal trend. Cumpston (*loc. cit.*) reared *N. insectifurax* through three generations on *P. atomaria* eggs in the laboratory. The wasps did not oviposit in *Chrysophtharta variicollis* eggs.

Dipterous parasitoids of paropsid larvae were recorded from the family Tachinidae (Goniinae:Blondeliini) and included *Anagonia anguliventris* Malloch, *Froggattimyia tillyardi* Malloch and *Paropsivora* spp. parasitizing *Paropsis* spp., and *Paropsivora australis* Macquart parasitizing *Chrysophtharta bimaculata* (Crosskey 1973; Tanton and Khan 1978). Cumpston (1939) described the

development of tachinid parasitoids in paropsid larvae, but was unable to obtain parasitization of larvae in captivity. Average seasonal levels of parasitism of larvae of various paropsid species have varied from 11% to 59% (P.B. Carne, unpubl. report; Tanton and Khan 1978). Greaves (1966) reported 20% parasitization of *C. bimaculata* larvae in a season of high larval population, followed by a 40% parasitization the following season when the larval population was very much reduced.

The hymenopterous species *Eadya paropsidis* Huddleston (formerly known as *Aridelus* sp.) and *Bracon* sp. (Braconidae) and *Tetrastichus* sp. (Eulophidae) have been recorded as primary parasitoids of paropsid larvae, while *Mesochorus* sp. (Ichneumonidae), an unidentified ichneumonid, and *Perilampus tasmanicus* (Cameron) (Pteromalidae) have been recorded as secondary or hyper-parasitoids (Huddleston and Short 1978; P.B. Carne, unpubl. report; Tanton and Khan 1978). *Mesochorus* sp. was a common parasite of the tachinid primary parasites. Hymenopterous primary larval parasites were recorded from *Paropsis* spp., but not *Chrysophtharta* spp. (P.B. Carne, unpubl. report). Average seasonal levels of parasitization of *P. atomaria* larvae by *Eadya paropsidis* of 9% to 37% were reported (Carne *loc. cit.*; Tanton and Khan 1978). Greaves (1966) found hyper-parasitization levels of tachinid parasitized larvae of *C. bimaculata* to range from 11% to 17%.

Tanton and Khan (1978) found adult *P. atomaria* beetles parasitized by a protozoan, *Pleistophora* sp., while Davies (1966) found some adult *C. bimaculata* beetles to be parasitized by mermithid nematodes.

Coccinellid beetles and their larvae have been reported to be

important predators of paropsid eggs and larvae. Tanton and Khan (1978) observed *Cryptolaemus montrouzieri* Mulsant, *Harmonia conformis* (Boisduval), *Rhizobius discolor* Erichson, *R. ventralis* Erichson and an unidentified *Rhizobius* sp. all feeding on eggs and/or larvae of *P. atomaria*. H.J. Elliott and D.W. de Little (unpubl. information) found *Cleobora mellyi* Mulsant and *Harmonia conformis* to be important predators of *C. bimaculata* eggs and larvae. Both species were successfully reared in the laboratory on a diet of *C. bimaculata* eggs, larvae of *C. mellyi* requiring 262 eggs and larvae of *H. conformis* requiring 212 eggs for complete development under standardized laboratory conditions. Average daily feeding rates of *C. mellyi* females were 21.0 eggs per day and of *H. conformis* females, 25.5 eggs per day. Adult *C. mellyi* were reported to consume an average of 11.24 *P. charybdis* eggs per day under laboratory conditions (P. Alma, *pers. comm.*). While field levels of predation of *C. bimaculata* eggs usually ranged from 20-40% (Greaves 1966; H.J. Elliott and D.W. de Little, unpubl. information), a large population of *C. bimaculata* eggs was reduced by 94% within 14 days of mass oviposition. Psyllids, which often occurred on the same trees as paropsids, were an alternative food on which coccinellid predators were observed to feed (Tanton and Khan 1978; H.J. Elliott and D.W. de Little unpubl. information).

Other predators included the pentatomids *Cermatulus nasalis* (Westwood) and *Oechalia schellenbergii* (Guerin-Méneville) which were recorded preying on eggs and larvae of *P. atomaria* (Tanton and Khan 1978) and of *P. charybdis* in New Zealand (Styles 1970). Styles also considered the European wasp, *Paravespula germanica* (F.) and birds such as starlings and sparrows to be important predators of *P. charybdis*.

A number of efforts have been made to introduce paropsid parasitoids into New Zealand for biological control of *P. charybdis*, including *Neopolycystus insectifurax*, *Froggattimyia tillyardi* and *Eadya paropsidis* (Clark 1938; J. Dugdale, unpubl. report; P.B. Carne, unpubl. report). These parasitoids were all collected from *P. atomaria* populations. More recent efforts have been made to locate and introduce tachinid parasitoids from endemic Australian *P. charybdis* populations (D.J. Albert, unpubl. report), but successful establishment has not yet been achieved (P. Alma, *pers. comm.*). Current efforts are involved with the introduction and establishment of the coccinellid predator, *Cleobora mellyi* H.J. Elliott and D.W. de Little, unpubl. information).

## 6. Approaches to the study of insect population ecology

### 6.1. Sampling methods

Morris (1960) described sampling as "a mixture of art, science, and drugery". Regardless of how sophisticated methods of analysing data and modelling insect populations may be, the raw census data still must be collected, and this often appears to be the least scientific aspect of the study of insect numbers. However, a scientific approach to sampling minimizes input costs and maximizes information output. Population sampling has been used for a wide range of purposes, including extensive surveys to predict damage levels to crops or forests, and very intensive surveys of the population dynamics of an insect species in a restricted area or plot.

In contrasting the Canadian work of Morris (1963) and co-workers on the spruce budworm, *Choristoneura fumiferana* (Clem.) with their own work on winter moth, *Operophtera brumata* (L.), Varley and Gradwell (1970) considered that if there were a choice between extensive and intensive studies, the intensive study in one place would be of prime importance. Although Morris sampled from many different places, no single place was sampled continuously, and it was not possible to distinguish between spatial and temporal effects. In contrast, the limiting of sampling to five oak trees in a mixed woodland enabled Varley and Gradwell to separate temporal and spatial differences and construct life tables for the population using either mean values for the five trees, or for each of the trees separately.

Many methods of sampling insect populations were discussed by Southwood (1966). Although population indices, such as evidence

of injury, frass drop and various traps have been employed, it has been considered (Morris 1960; Southwood *loc. cit.*) that for long-term, intensive studies direct counts of individuals on samples of known size can only meet all the objectives. An important consideration in the use of direct sampling methods is whether the estimation of population intensity, i.e. an expression of numbers in terms of their food supply or living space (e.g. leaf or shoot), or absolute population, i.e. an expression of numbers in terms of a non-varying unit (e.g. area) is required. Morris (1960) considered that the absolute unit was essential for long-term population dynamics as it afforded a stable unit for frequent sampling to enable development of life tables. In their studies of the population dynamics of defoliating insects, Klomp (1966), Morris (1955) and Richards and Waloff (1961) sampled on the basis of a foliage unit and subsequently determined the number of such units per unit of land area to obtain absolute estimates.

An effective sampling plan pre-supposes some knowledge of the distribution of the insect population under study in space and time. A completely random spatial distribution of insects in nature appears to be rare; populations usually are "over-dispersed" and their frequency often approximates the negative binomial distribution. Lyons (1964) found that the distribution of egg clusters of the sawflies *Neodiprion swainei* Middleton and *N. sertifer* (Geoffroy) within trees was affected by the females' preference for well illuminated oviposition sites. Carne (1966) considered that the distribution of egg batches among trees, of the paropsid *Paropsis atomaria*, was determined by the females' presence for oviposition close to foliage suitable for larval

feeding and to other egg batches. Populations of adults of the chrysomelid *Phytodecta olivacea* (Forster), larvae of the sawfly *Neodiprion sertifer*, immature stages of the cabbage looper *Trichoplusia ni* (Hubner), and eggs of the paropsid *P. atomaria* were all reported to have frequencies approximating the negative binomial distribution (Richards and Waloff 1961; Wilson and Gerrard 1971; Harcourt 1965; Carne *loc. cit.*).

The selection of the sample unit is an important consideration in the sampling plan. Morris (1955) laid down six broad criteria for the sample unit:

1. It should be of such a nature that all units in the sampling universe have an equal chance of representation.

2. It must have stability (i.e. the number of units available to the insect population must not be affected by changes in growth habits in the plant).

3. The proportion of the insect population using it as a habitat must remain constant.

4. It should be small enough so that sufficient units can be examined on a given plot and date to provide an adequate estimate of variance.

5. In absolute population work it should be readily convertible to a unit area basis.

6. It should be easily delineated in the field, such that there is not a serious loss or disturbance of the insect population.

In detailed studies of population dynamics, Morris (1960) considered the two main objectives were to estimate mean population density in a small area (or restricted universe) and to estimate

survival (or mortality). Population density was an important variable affecting survival, and survival estimates were desirable not only for each generation, but for shorter age intervals (stages) within generations. In designing a sampling programme it would therefore be necessary to consider three aspects: the selection of the sampling universe (dependent on objectives); the selection of the sample unit, and the determination of optimum stratification and distribution of units within the selected universe. Morris and Harcourt (1969) both considered that small, carefully stratified units yielded the most efficient design. Since a relatively large variation usually occurred between the sample units in natural populations, there was little point in achieving a degree of accuracy in sample estimation out of all proportion to the precision of population estimation by the sampling method employed. For intensive population studies, an acceptable degree of sampling precision adopted by most investigators has been a ten percent standard error (Morris 1960; Southwood 1966; Harcourt 1969).

In his study of the distribution and dispersal of *P. atomaria*, Carne (1966) sampled populations by recording the stages present on 50 tagged shoot units in each study site. An eucalypt shoot unit was defined as a branchlet terminating in 50-70 ultimate shoots 3mm or less in diameter, which was the preferred oviposition site of the species. Study sites were located in plantations of regularly spaced trees three to seven metres tall, and dominant shoot units were tagged on both sides of the trees in each row at heights convenient for close inspection. Study sites were sampled at intervals of two or three days in summer, and at

intervals of up to seven days as larval growth rates declined in the autumn. At each time of sampling, the numbers of egg batches and fourth instar larvae, and the presence or absence of younger larvae, were recorded. Carne found that the number of shoot units bearing each stage could be taken as a measure of the relative abundance of each stage. While it was easy to count egg batches and fourth instar larvae, the counting of younger larvae was prohibitively slow, due to their smaller size, greater number, and intense colonial behaviour. Since it would be expected that the distribution of partly grown larvae would be intermediate in nature between that of the egg and that of the final instar larva, changes of younger larval shoot occupancy would adequately measure their changing abundance. Using this sampling procedure, Carne plotted population intensities of eggs and each larval instar at one study site over four seasons.

Madden and Bashford (1977) in a study of the population biology of the geometrid defoliator (*Chlenias* sp.) of *Pinus radiata* D. Don in Tasmania, used a destructive method of sampling in which shoots were removed and transferred in plastic bags for detailed census in the laboratory. A minimum number of 20 shoots (15cm long lateral shoot) per tree was examined for the presence of *Chlenias* sp. before that tree was rejected and a new one chosen. A new tree was selected after the location of an infested shoot. The result of this system of sampling was that a larger number of trees was examined in the early and late stages of the larval period, whereas when population intensity was at its peak, in mid-season, only 20 trees were required to obtain the requisite number of 20 samples from each study area. Advantages of the

destructive system of sampling were that material could be more thoroughly evaluated and parasitization and/or disease estimated by dissection.

## 6.2. Population studies

### 6.2.1. The life-system

The "life-system" approach to the study of insect populations has been proposed by Clark (1964c), Geier (1964) and Clark *et al.* (1967). This approach was based on the concepts of "population" and "environment" developed by Solomon (1949), in which both were seen as inseparable components of an ecosystem. Thus the life-system of species was regarded as "that part of the ecosystem determining the existence of a species population, and including the subject population and its effective environment" (Clark *et al., loc. cit.*). Many of the difficulties of the approaches of Nicholson (1954, 1957, 1958), Andrewartha and Birch (1954, 1960) and Milne (1957a, b, 1962) to the study of insect populations were thus overcome by this integrated and functional approach.

The construction of population curves, in which population frequency, or density, or its logarithm (Morris 1960) is plotted against time or physiological time (Hughes 1972, 1973) gives an overall estimate of population size (Clark *et al.*, 1967; Varley *et al.*, 1973). Population curves of successive developmental stages in a single generation reflect the influence of seasonal ecological processes which may be additive (such as the increase of environmental resources, immigration, increased reproduction and development and limitation of natural enemies), or subtractive

(such as intraspecific competition, predation and parasitization, and unfavourability of environmental agencies). The nett result of the interaction of these processes is population fluctuations in time. Morris (1957) considered that, in interpreting mortality data, variation over time was the important attribute of mortality, and that low but variable mortalities may have more influence on the population trend than high but relative constant mortalities. The sequence in which mortalities occurred, and the magnitude and extent of the interaction of mortality contributed by various contemporaneous factors (Morris 1965) were also important factors in explaining why low but variable mortality may act as the primary determinant of population trend.

Clark *et al.* (1967) considered that the main objective in the study of natural populations was to learn enough about their functioning to devise efficient ways of manipulating them as desired. The possibility of gaining an adequate understanding of natural populations was sometimes questioned because of the multiplicity of ecological events and processes in the life-system of any subject species conceivably affecting its population numbers. However, recent work supported Morris' (1959) hypothesis that a few "key" influences, operating usually in one or two critical age intervals, could very largely determine population trend. Clark *et al.* listed three main approaches to the study of insect life-systems: "life-table" studies, "key-factor" studies, and the study of ecological processes. The aim of life-table studies was to follow the change in population density for each developmental stage or age interval of the insect as a function of the independent variable operating during each age interval. This type of approach

was adopted by Richards and Waloff (1961) and Klomp (1965). Key-factor studies, in which the change in population by generation, measured at one specific point in the life-cycle, is modelled as a function of the key variables determining numerical change, irrespective of the particular stage(s) affected by them was used by Morris (1959, 1963). Varley and Gradwell (1968) developed this approach graphically from the preparation of life-tables as a series of annual population budgets. Finally, the study of ecological processes, in which the aim was to describe the modes of operation of particular independent variables, has been the approach adopted by Clark (1962, 1963a, b, c, d, 1964a, b, c) and Clark and Dallwitz (1974, 1975).

### 6.2.2. Life-tables

Richards (1961) considered the life-table to be the "keystone of all population studies" because it provides numerical estimates of the successive causes of mortality. The most frequently used type of life-table in insect population dynamics is the "age-specific" life-table (Southwood 1966) which is based on the fate of a cohort of individuals in a particular generation. Richards (1961) adopted the term "budget" to describe an age-specific life-table which listed the actual absolute populations at different stages and recorded the action of mortality factors where these were known. Harcourt (1969) has stressed that a life-table is not an end in itself, but merely systematizes the presentation of survival and mortality data in populations:

> "One or two such tables will reveal only that high mortalities may occur at certain age intervals, but a

sequence of tables, suitably replicated in time and place, should increase our understanding of the dynamics of an insect population and at the same time reveal the most opportune periods for management so as to influence survival rates."

Fundamental to the establishment of a life-table is an adequate programme of sampling that measures the size of the population, and the proportion of each stage or instar in it. Richards (1961) stressed that sampling intervals should be short enough to allow for very rapid growth during some seasons and also for weather variations, but regular and prolonged over the whole season so that each form is sampled in proportion to its abundance. Harcourt (1969) considered that the timing of samples was particularly important in assessing rates of mortality from parasite attack and mortality was the product of apparent parasitization and host density per unit area. These estimates represented potential and not actual values, since the removal of the host interfered with the natural course of events, and the ultimate fate of parasitized larvae in the field would not be known. Since it is usual for a single census count of a stage to provide a figure for the total number of insects entering that stage, such statistics must normally be obtained indirectly from the population curve. This inevitably involves some method of integration of population curves (Harcourt 1969). Several methods for estimating numbers entering a stage have been proposed (Southwood and Jepson 1962; Waloff and Bakker 1963; Richards and Waloff 1954, 1961; Richards, Waloff and Spradbery 1960; Dempster 1956, 1961; Kiritani and Nakasuji 1967). A basic approach was

used by Southwood and Jepson (*loc. cit.*) who determined the population at the median age of a stage by the summation of a series of graphical estimates, the total of which was divided by the mean developmental time under field conditions. Mortality between stages was then estimated by subtraction of median age population estimates of successive stages. The method underestimated the population, as individuals destroyed, for example by predation, were present for less than the full developmental time. However, if the bulk of the mortality occurred at the end of the stage, the population estimate given by the method would approach the number entering the stage.

### 6.2.3. Physiological time

Davidson (1944) introduced the concept of physiological time when he plotted the developmental time (incubation period) of eggs of the fruit fly, *Drosophila melanogaster* Meigen, at a number of constant temperatures. The relationship of developmental time to temperature was found to be exponential over the range of temperatures normally encountered by the developing insect. Using this relationship, it was possible to estimate the developmental time, or number of "day-degrees" required for complete development of individuals in a given stage.

Temperature development curves were used by Guppy and Mukerji (1974) and Taylor and Harcourt (1978) to predict the appearance of successive stages of the alfalfa weevil, *Hypera postica* (Gyll.) and the asparagus leaf beetle, *Crioceris asparagi* (L.), respectively, in the field. In drawing up life-tables for the cereal leaf beetle, *Oulema melanopus* (L.), Helgesen and Haynes (1972) considered

Southwood and Jepson's (1962) method of integrating population curves the most appropriate for their study due to the protracted oviposition period and the consequent simultaneous occurrence of all stages. Developmental rates at different temperatures were determined in the laboratory and graphed. Developmental time in the field was estimated by determining the average temperature affecting each age class during the generation and reading the corresponding developmental times directly from the graphs.

### 6.2.4. Computing methods

The application of computing methods to insect population dynamics has provided new techniques for estimating the survivorship of stages in insect populations (Manly 1974a, b; Ruesink 1975; Birley 1977). These methods allow a more flexible sampling programme in which the sampling error (as a percentage of the mean) should not exceed twice the number of non-zero data points (Ruesink 1975). For example, given ten sampling dates on which the density was non-zero, then on each date enough samples should be taken to ensure a standard error within twenty percent of the mean. Hence, frequency of sampling assumes relatively less importance. The methods reconstruct the discrete survivorship function in physiological (developmental) time. Stage recruitments, durations, and mortalities may then be estimated.

## 6.3. Key factors and population processes

Nicholson (1954) proposed that populations naturally tended to exist in a state of "equilibrium" or "balance" and that prolonged equilibria were attributable to the action of regulatory

density-dependent mortality processes. Morris (1959, 1963b) proposed that variations in populations from one generation to the next were largely the result of certain mortality factors described as key-factors. Varley (1963), Klomp (1966) and Southwood (1966, 1967) distinguished between density-dependent processes which had a stabilizing effect on populations, and key-factors, which had a disturbing effect. Richards and Southwood (1968), and Harcourt (1971) suggested that the same factor may have both effects.

Harcourt (*loc. cit.*) found that adult migration, the regulatory factor in the population dynamics of *Leptinotarsa decemlineata*, in eastern Ontario, acted immediately in a density-dependent manner, but was over-compensating in its action; this lack of precision was a regular form of disturbance leading to population fluctuations. Weather conditions appeared to have little effect on populations of *L. decemlineata*, and the only natural enemy, a tachinid parasitoid, showed an inverse density-dependent relationship with its host. This parasitoid may have regulated the beetle population in its original habitat, but with the intensive cultivation of potato, which greatly increased the beetle's food resource, *L. decemlineata* was able to increase its population to a level where the parasitoid was unable to cope with further increase. Since *L. decemlineata* was without a density-related mechanism to assist in the conservation of food resources by maintaining low numbers, numbers increased until mass starvation of larvae and emigration of surviving adults occurred, this latter process supplying the density-dependent regulatory factor. With the annual perpetuation of food resources (by man),

surviving local adults renewed the local populations with numbers rising and falling in cycles of increasing amplitude.

The majority of studies of insect life-systems have been of insects of economic importance. Such insects are either pests, or biological control agents whose habitat has been manipulated by man's activities. This manipulation has often resulted in creation and maintenance of unstable (ruderal) habitats (Grime 1977). Phytophagous insects in such habitats are highly r-selected and the populations of these insects lack effective regulation by density-dependent mechanisms (Southwood *et al.* 1974).

Natural enemies (predators, parasites and pathogens) are density-dependent mortality factors which may act as key-factors, particularly in the situation where an insect is (inadvertently) introduced in a new country. Neilson and Morris (1964) considered that larval parasitoids, introduced as biological control agents, had been largely responsible for regulating Canadian populations of European spruce sawfly, *Diprion hercyniae* (Htg.) first detected in Canada in 1930.

With populations of the native chrysomelid, *Phytodecta olivacea*, in Britain, Richards and Waloff (1961) considered that predators, especially mirid bugs, exercised most control of the population. These mirids did not appear to act in a density-dependent manner, however, and were observed to have alternative food sources in the form of aphids and psyllids. Carne (1969) considered that a tachinid parasitoid achieved only partial control of populations of the eucalypt-defoliating sawfly, *Perga affinis affinis*.

With respect to the paropsids on eucalypts, Greaves (1966) and P.B. Carne (unpubl. report) found little evidence to suggest

that parasitoids acted as key-factors. Greaves (*loc. cit.*) found parasitization by the tachinid parasitoid of *C. bimaculata* to be markedly influenced by the effects of a hyperparasitoid. However, Greaves (1966), P.B. Carne (unpubl. report) and H.J. Elliott and D.W. de Little (unpubl. information) considered that predation both by insectivorous birds, and by coccinellids, was possibly of considerable significance in the regulation of host abundance.

Direct effects of weather have been considered to be the key-factors in the population dynamics of a number of insect species. Silver (1963) and Schmiege (1966) associated collapse of populations of the black-headed bud-worm, *Acleris variana* (Fern.), with cold, wet or hot, dry extremes in summer weather. Foltz *et al.* (1972) considered unfavourable weather during the larval and adult dispersal periods of the jack-pine bud-worm, *Choristoneura pinus* Freeman, was the key-factor causing population collapse. The effects of heavy summer rain, in significantly reducing populations of the sawfly *Neodiprion swainei*, were investigated by Philogène (1972), who showed a considerably increased mortality due to physical effects of removal of larvae from foliage. A decreased rate of larval development was also observed. Greaves (1966) and P.B. Carne (unpubl. report) reported greatly reduced populations of *C. bimaculata*, *C. cloelia* and *P. atomaria* due to the effects of dislodgement of immature stages by violent summer rain and hail storms.

The availability of food resources may act directly as a key-factor in certain insect populations. Dempster (1971) found that the positive growth of populations of cinnabar moth, *Tyria jacobaeae* L., was limited by food supply of the host-plant,

ragwort, *Senecio jacobaeae* L. Starvation led to a population collapse and the rate of recovery after this collapse was dependent on rapid recovery of ragwort plants. Greaves (1966) considered that starvation due to intensive defoliation by very dense populations, caused considerable mortality in *C. bimaculata* populations in two summers.

Mortality factors have been observed to act in combination to control insect populations. In a study of the eucalypt-defoliating phasmatid, *Didymuria violescens*, Readshaw (1965) found that two systems of control operated on population. At low density, increase was limited largely by predators and parasites, but at high density, increase was limited ultimately by intra-specific competition for food. Very cool summer weather conditions occasionally disrupted the low density system of control and thereby initiated outbreak release. This system has obvious similarities to the control system proposed by Harcourt (1971) for *Leptinotarsa decemlineata*; in the latter case, man's perpetuation of potato monocultures is the disruptive influence initiating outbreak release.

White (1978) has taken an extreme position, in proposing that for most animals, the single most important factor limiting their abundance is a relative shortage of nitrogenous food for the young, growing individuals. This viewpoint was developed from a study of outbreaks of the psyllid *Cardiaspina densitexta* Taylor in South Australia, in which White (1969) developed a stress index based on a comparison of summer and winter rainfalls to measure weather-induced stress of the host eucalypt. The physiological stress of trees, as a result of water deficit

induced by drought or waterlogging, was postulated to increase the amount of nitrogenous food available in the foliage, to psyllids, thus greatly increasing the chances of survival and reproduction.

White (1969, 1973, 1974, 1976) correlated a high stress of plants with outbreaks of a number of phytophagous insects, including the paropsid *P. charybdis*, in New Zealand. Since its introduction into New Zealand about 1916, White (1973) observed that *P. charybdis* had undergone several major fluctuations of population in spite of the fact that there was no apparent evidence of the significant action of mortality factors such as shortage of food or natural enemies. Each major outbreak of population had corresponded with a new wave of colonization, but there was no apparent explanation for subsequent decline as the food resource did not appear to be a limiting factor. White, in observing the close correlation between stress index and population size and spread of *P. charybdis*, suggested that the food resource became relatively less available during periods when the stress index was negative, due to low nitrogen content. Subsequent work on the feeding relationships of *P. atomaria* (Fox and Macauley 1977) has shown that growth of larvae was directly and more closely related to the nitrogen content of eucalypt leaves than to the expected inverse relationship with tannin and phenolic content.

It has been argued that purely numerical studies have been too narrow to understand fully the processes operating in the maintenance of insect populations in space and time (Price 1971b). The numerical approach, involving considerable expenditure of effort in sampling procedures, has often forced workers to resort

to correlation, due to lack of data relevant to an understanding of processes based on direct biological observations. The life-system approach of Clark *et al.* (1967) has provided a more integrated approach to the study of insect populations. Following this approach, Clark and Dallwitz (1974, 1975) have been able to provide quantitative measurements of extremely intimate insect-host relationships in their studies of psyllid populations on *Eucalyptus blakelyi*.

Price (1971b) defined three broad approaches towards holistic insect population studies:

1. "The study of individual insects will suggest the adaptive nature of their morphology, physiology, and behaviour, and furnish an insight into the critical factors to which they respond in the environment."
2. "Observations made on groups of populations will identify variations in time and space between populations that are subject to selection, and that could lead to more or less endogenous population control processes."
3. "The study of insects in a community will show how the organization within this unit influences individuals and populations of particular species, and the result of interactions between species."

This approach would thus enable the development of a study programme with survival of the reproductive individual as the central theme, and with the emphasis switched from the study of numerical change, to the study of adaptation and evolution of populations.

# SECTION III - A TAXONOMIC REVIEW OF THE TASMANIAN *EUCALYPTUS*-DEFOLIATING PAROPSIDS

## 1. Introduction

Essential prerequisites to ecological studies of the Tasmanian *Eucalyptus*-defoliating paropsids were:-

1. an evaluation of the extent and distribution of the paropsid fauna,
2. the identification of component species,

and, 3. the association of the immature with the mature stages.

The following work is intended as a preliminary taxonomic review which will enable the identification of the Tasmanian species, at least to a code designation, if not to an actual name. Comparative studies between genera are minimal since only a small proportion of the species in each genus represented occurs in Tasmania. Studies of pupal characteristics are omitted, since this soil-borne stage is inconspicuous.

No attempt has been made to designate type material or describe new species. It is considered that a more detailed study of the whole Australian fauna will be necessary before such steps will serve to clarify the current state of nomenclatural chaos in the group.

Voucher specimens will be lodged in the Australian National Insect Collection, Canberra.

## 2. Materials and Methods

### 2.1. The survey

The main island of Tasmania, lying between 40° 40' and 43° 40' S, and 144° 40' and 148° 20' E was sampled for *Eucalyptus*-defoliating paropsids between December 1972 and March 1978. Sampling was conducted from sea level to the tree-line which was at an altitude of approximately 1,300 m. Access was mainly gained by the road network, and the only area not covered was the south-west region where there are few roads. Since this region supports only three species of eucalypts, *E. nitida*, *E. vernicosa*, and *E. ovata* (Jackson 1965), and these species and their characteristic associations are well represented in other regions, this was not considered a major omission.

### 2.2. Sampling methods

The presence of adult beetles, larvae and eggs was determined by direct observation of foliage of young sapling eucalypts up to five metres in height, and by searching under bark of both young and mature eucalypts, and in the leaf and bark litter beneath trees. A one metre square beating tray was used to gain a relative assessment of adult densities and species proportions. Whole saplings or their branches were vigorously shaken, and adults falling on to the tray were collected while still displaying the immobile "shock" reaction.

Native host eucalypts on which paropsids were collected were identified using keys and descriptions provided by Curtis and Morris (1975). Jackson's (1965) eucalypt distribution maps were

also employed (Inside back cover, Vol. I). Code designations for eucalypts, developed by Pryor and Johnson (1971) were used in the occurrence notes accompanying species descriptions. All eucalypt species collected from, and their respective codes, are shown in Table 1. The codes are information rich, showing current taxonomic opinion on the relatedness of species.

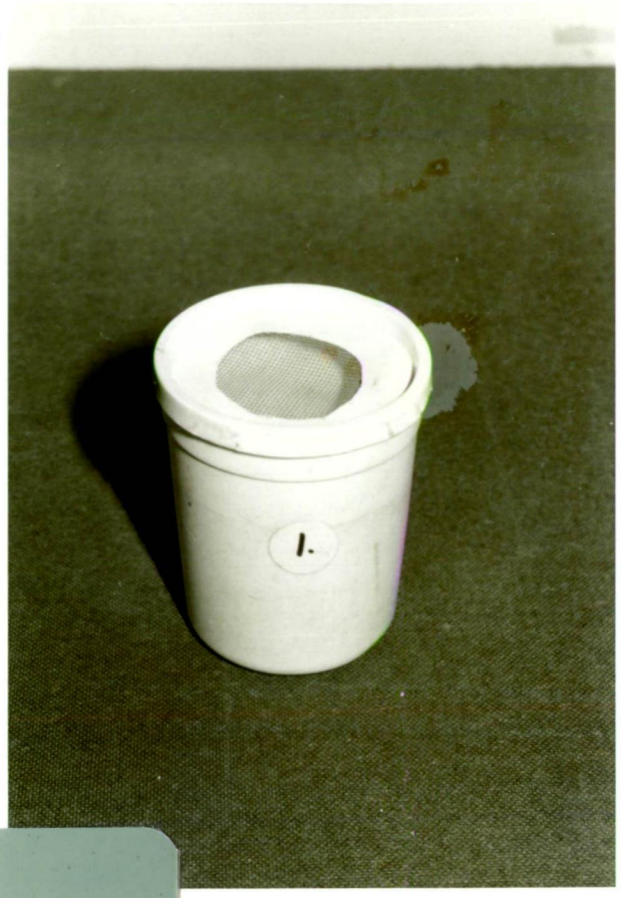
## 2.3. Collecting methods

Plastic food containers manufactured by Vinyl Clad (Australia) (20Y-R6) (Fig. 1) were utilized as useful, general purpose collecting containers for live material. A circular area, 5 cm in diameter, was cut from the press-on lid, and nylon mesh netting was glued over the hole. This provided adequate air circulation, which was essential, as both adult and larval stages were particularly sensitive to changes in temperature and humidity. The containers held up to 50 beetles, or an equivalent number of larvae, together with a few leaves for food. When containers were filled they were labelled and stored in shade until they were transported to the laboratory.

In the laboratory, specimens were either kept alive for photographing, identification or breeding from, or representative specimens were killed and placed in the collection.

## 2.4. Preservation of specimens

Adults were killed either in an ethyl acetate killing jar, or by freezing. The latter method was preferred, since there was no interference of organic solvent with the natural body pigments. However, even with freeze-killing, it was impossible to preserve the live-colours of many species.




1

2

Figs. 1, 2: Containers for (1) collecting, and (2) rearing paropsid adults and larvae.

Table 1.

List of *Eucalyptus* species on which Tasmanian paropsid species were collected.

| Species | Code* |
|---|---|
| *obliqua* L'Hérit. | MAKAA |
| *delegatensis* R.T. Bak. | MAKBE |
| *regnans* F. Muell. | MAKCA |
| *sieberi* L. Johnson | MAKED |
| *pauciflora* Sieb. ex Spreng. | MAKHA |
| *risdonii* Hook. f. | MATEB |
| *tenuiramis* Miq. | MATEC |
| *pulchella* Desf. | MATEG |
| *amygdalina* Labill. | MATEH |
| *nitida* Hook. f. | MATEJ |
| *coccifera* Hook. f. | MATES |
| *diversicolor* F. Muell.† | SEB:A |
| *ovata* Labill. | SPEAB |
| *rodwayi* R.T. Bak. and H.G. Sm. | SPEAH |
| *nitens* (Deane and Maid.) Maid.† | SPIFG |
| *globulus* Labill. | SPIFL |
| *vernicosa* Hook. f. | SPIJA |
| *viminalis* Labill. | SPIKK |
| *dalrympleana* Maid. | SPINC |
| *rubida* Deane and Maid. | SPINF |
| *gunnii* Hook. f. | SPINI |

*After Pryor and Johnson (1971)

†Introduced species grown in plantation.

Dried adult specimens were pinned on "Asta" gauge 3 stainless steel entomological pins, labelled with locality and data of collection, and host species on which the specimen was collected (where applicable). Each specimen was labelled with a code (Section 2.6). Specimens were stored in unit trays in a standard metal entomological cabinet (Norris and Upton 1974).

Larvae were killed in KAA fixative [77% ethanol; 15.3% glacial acetic acid; 7.7% kerosene (Norris and Upton 1974)], and transferred to 80% ethanol after several hours for permanent storage. Larvae of each species were stored in separate air-tight screw-top glass vials and labelled with a code.

## 2.5. Rearing methods

Immature stages were bred from adults, and adults reared from immatures in the laboratory, so that adults, eggs and larvae could be matched in the field and identified. Where possible, each species was maintained on the foliage of the host eucalypt species on which it was collected. If quantities of this foliage were not readily available, foliage of the most closely related eucalypt species which was readily available was substituted.

Material was either reared in plastic petri dishes (9 cm diameter by 1 cm) on foliage which was changed daily, or in rearing chambers (Fig. 2). Rearing chambers were manufactured from one litre capacity plastic screw-top bottles (A.C.I. Y23-101 8-40 SR), with neck and top removed, glued with Selley's "Kwik-Grip" on inverted plastic flower-pots (8 cm diameter base, 12.5 cm diameter top; L.J. Wallace Pty. Ltd., Lidcombe, N.S.W., manufacturer). A portion of the side of the flower-pot was cut

Table 2.

Tasmanian *Eucalyptus*-defoliating paropsid genera and species.

| | | (Code - D.W. de L.) |
|---|---|---|
| 1. | *Paropsis* Olivier | |
| | 1. *tasmanica* Baly | Ps5 |
| | 2. sp. | Ps9 |
| | 3. *charybdis* Stål | Ps4 |
| | 4. *dilatata* Erichson | Ps6 |
| | 5. sp. | Ps7 |
| | 6. *incarnata* Erichson | Ps8 |
| | 7. *rubidipes* Blackburn | Ps2 |
| | 8. *porosa* Erichson | Ps3 |
| | 9. *aegrota* Boisduval | Ps1 |
| 2. | *Trachymela* Weise | |
| | 1. sp. | Ta7 |
| | 2. sp. | Ta2 |
| | 3. *rugosa* (Chapuis) | Ta5 |
| | 4. sp. | Ta4 |
| | 5. *papulosa* (Erichson) | Ta1 |
| | 6. sp. | Ta8 |
| | 7. sp. | Ta6 |
| | 8. sp. | Ta3 |

Table 2. (Continued)

| | | (Code - D.W. de L.) |
|---|---|---|
| 3. | *Chrysophtharta* Weise | |
| 1. | *lignea* (Erichson) | Ch9 |
| 2. | *aurea* (Blackburn) | Ch3 |
| 3. | *decolorata* (Chapuis) | Ch4 |
| 4. | *agricola* (Chapuis) | Ch2 |
| 5. | *variicollis* (Chapuis) | Ch7 |
| 6. | *bimaculata* (Olivier) | Ch1 |
| 7. | sp. | Ch12 |
| 8. | sp. | Ch13 |
| 9. | sp. | Ch8 |
| 10. | *nobilitata* (Erichson) | Ch5 |
| 11. | sp. | Ch11 |
| 12. | *simsoni* (Blackburn) | Ch6 |
| 13. | sp. | Ch10 |
| 4. | *Paropsisterna* Motschulsky | |
| 1. | *nucea* (Erichson) | Pa1 |
| 2. | *morio* (F.) | Pa3 |
| 3. | *rufipes* (F.) | Pa2 |
| 5. | *Sterromela* Weise | |
| 1. | *lineata* (Marsham) | Sa4 |
| 2. | *subcostata* (Chapuis) | Sa1 |
| 3. | *trimaculata* (Chapuis) | Sa2 |
| 4. | sp. | Sa3 |

away and a 2.5 cm diameter by 10 cm glass vial glued with "Araldite" to the inner surface, adjacent to the cut margin. A hole of diameter 0.3 cm, just large enough to allow the passage of the stem of a eucalypt shoot was drilled through the base of the bottle so that it was aligned with the glass vial, and one of the drainage outlets in the base of the pot. The lid of a 9 cm diameter plastic petri dish, into which had been inserted a wire gauze covered ventilation hole, was used as a cover for the chamber. Shoots were placed in these rearing chambers so that the cut end was passed through the hole at the base of the chamber, and into the water-filled vial supported by the inverted flower-pot. The advantage of using rearing chambers was that it was necessary to change foliage only every third day.

For pupation, prepupae were transferred to clean petri dishes and placed on filter paper discs.

2.6. Identification of specimens

Adult specimens were readily keyed out to genera using the generic key provided by Weise (1901), and subsequent generic descriptions by Weise (1901, 1908, 1915). Within each genus, adults and matched larvae of each species were given code numbers (Table 2).

The keys and descriptions provided by Blackburn (1896, 1897, 1898a, b, 1899, 1901, 1906) were mostly used for the identification of adults. Adult specimens were forwarded to Dr B.J. Selman, who is currently working on the taxonomy of Australian Chrysomelinae, for comparison with specimens held in the British Museum (Natural History). Formal identification of species was only made in cases of absolute certainty. No attempt was made to name unidentified

specimens, due to the as yet unpublished current review of the whole Australian paropsid fauna.

Larval keys and descriptions provided by Cumpston (1939) were used in the identification of two species.

## 2.7. Description and illustration of species

Since the following work is not intended as definitive taxonomy, but is rather a preliminary review of the species which occur in Tasmania, descriptions only include easily observable characteristics which separate and identify the Tasmanian species. All descriptive entomological terms used may be found defined in de la Torre-Bueno (1973).

Because of the transience of the most readily identifiable characteristic of many species, the colours in life, and of the paucity of other morphological characteristics, colour illustrations of live specimens were considered a necessary adjunct to identification. Photographs were taken in the laboratory using Kodachrome colour negative film, a "Pentax SP 1000" camera and "Takumar" 50 mm macro lens. Black and white photographs were taken using Ilford film (ASA125). Specimens were illuminated by two "Atlas daylight" 8 W fluorescent tubes. Where possible, fresh eucalypt leaves of the preferred host were used as background. Excessively mobile specimens were anaethesitized with ether.

All line drawings of specimens or of their organs were done with the aid of an "Olympus" stereo-microscope with an objective magnification range of 0.7 to 4 x and eyepieces with 20 x magnification. A 100-division graticule was used in one eyepiece. 2H pencil was used for sketching, and sketches were inked in with a "Rotring isograph", drawing pen using Indian ink and 0.18, 0.25 and 0.35 "Rotring isograph" nibs.

3. The *Eucalyptus*-defoliating paropsid genera represented in Tasmania

The Tasmanian *Eucalyptus*-defoliating paropsid species are found in five genera, *Paropsis* Olivier [*sensu stricto* (Weise 1901)], *Chrysophtharta* Weise, *Paropsisterna* Motschulsky, *Sterromela* Weise, and *Trachymela* Weise. Weise (1915) placed these genera, together with several non-*Eucalyptus*-defoliating genera in two tribes, the Paropsini, which included *Paropsis, Chrysophtharta, Paropsisterna* and *Trachymela,* and the Dicranosternini, in which *Sterromela* was relegated. With respect to the present study of the Tasmanian representative species of these genera, this tribal division is somewhat arbitrary, since it is based entirely on the single character of the presence or absence of cilia on the epipleuron. In the present study, therefore, all species are regarded as belonging to a single taxon, and referred to as "paropsids", which recalls the original name,"Paropside", given by Olivier (1807).

A total of 37 species of paropsids were encountered on eucalypts in Tasmania in the present study. Certain identification of only 23 of these species was possible(Table 2). According to B.J. Selman (*pers. comm.*), many paropsid species have highly variable geographic races and polymorphic forms, similar to the chrysomelid tree defoliators of North America (Brown 1959). Tasmanian forms may therefore represent sub-species of species of wider mainland Australian distribution. The relatively recent isolation of Tasmania from the mainland continent [12,000-13,500 B.P. (Jennings 1971)] may not have allowed sufficient time for complete speciation to have occurred in many instances, e.g. *P. incarnata* in Tasmania and its allopatric species/form, *P. atomaria* in S.E. mainland Australia.

*Paropsis s.s.* has been the genus most thoroughly studied and is consequently best known. Weise (1916) listed a total of 64 species in this genus (Table 3). Of the nine species of *Paropsis* encountered in Tasmania in the present study, seven were identified. Thus, about eleven percent of the known species of *Paropsis* are represented in Tasmania.

The genus with the most species in Tasmania, *Chrysophtharta*, is far less well known. This is mainly because the bright colours which so readily identify the adults of the species of this genus when alive, fade on death, leaving uniformly pale brown species with an absolute paucity of readily identifiable morphological characters. Blackburn (1899) found species in this group to be the most difficult to identify of all paropsid species, and was tempted to omit them from his revision. Weise (1916) listed a total of 44 species in this genus (Table 3). Of the thirteen species encountered in Tasmania in the present study, eight were identified; this representing about eighteen percent of the known species of *Chrysophtharta*.

Another very difficult genus in which many virtual sibling species occur, is *Trachymela*. This is the largest paropsid genus, containing 121 described species (Weise 1916) (Table 3). Eight species were encountered in Tasmania in the present study, but only two were identified with certainty. A further three species were doubtfully linked with names recorded from Tasmania. This total of five species represented only four percent of the total recorded species of *Trachymela*.

Weise (1916) separated the genus *Sterromela* from *Paropsisterna*, placing the former genus in the "Dicranosternini" on the basis of the ciliate epipleuron. He included four species in *Sterromela*.

Table 3.

Representation of *Eucalyptus*-defoliating paropsids in each genus in Australia (Weise 1916) and in Tasmania.

| Genus | Australian Total (Weise 1916) | Tasmanian Total (Weise 1916) | Tasmanian Total (Present study) | Tasmanian Total Identified (Present Study) |
|---|---|---|---|---|
| *Paropsis* | 64 | 8 | 9 | 7 |
| *Trachymela* | 121 | 4 | 8 | 2 |
| *Chrysophtharta* | 44 | 13 | 13 | 8 |
| *Paropsisterna* | 55 | 4 | 3* | 3* |
| *Sterromela* | 4 | 1 | 4* | 3* |

**P.lineata* (Marsham) (Weise 1916) transferred to *Sterromela* in present study.

The separation of *Sterromela* from *Paropsisterna* is well founded, since the larvae of these two genera are quite distinct, larvae of *Sterromela* resembling *Trachymela* larvae, while larvae of *Paropsisterna* are distinguished by their dense setae. The Tasmanian species, *Paropsisterna lineata* (Marsham) therefore clearly belongs in *Sterromela*, as may many other species of *Paropsisterna* which only occur on mainland Australia. Weise (*loc. cit.*) listed a total of 59 described species in the two genera. Six species have been identified in Tasmania in this study (Table 3). A seventh "species" is probably more correctly a polymorphic form. Thus about ten percent of the known species of *Paropsisterna* and *Sterromela* are represented in Tasmania.

*Trachymela* appears to be a successful genus throughout the full range of its Australian distribution, but it is poorly represented in Tasmania where only four percent of the species occur. Conversely, *Chrysophtharta*, with only about one-third the species of *Trachymela* Australia-wide has about twenty percent representation in Tasmania. This suggests that *Trachymela* is better adapted to the generally warm, arid climate of much of Australia, while species of *Chrysophtharta* prefer the relatively cool temperate climates of S.E. and S.W. Australia, and particularly, of Tasmania. In Tasmania, species of *Trachymela* are most frequently encountered in relatively extreme environments such as in sub-montane habitats or on eucalypt species with particularly thick and tough foliage (e.g. *Eucalyptus vernicosa*, *E. rodwayi*), suggesting an adaptation of this genus to harsher conditions. The secretive habit of the larvae of most *Trachymela* species of concealing themselves under bark during day-time supports the fore-going hypothesis.

Species of the genera *Chrysophtharta* and *Paropsis* are typically cool-temperate forest and woodland species. The larvae feed exposed on foliage in the day-time, sometimes in large, gregarious groups. Several species are capable of building up large populations and causing heavy defoliation. One species in particular, *C. bimaculata* (Olivier), attacks eucalypts of the subgenus *Monocalyptus*, series Obliquae, which are the commercially important species of the Tasmanian forest industry. *C. bimaculata* periodically undergoes widespread population outbreaks in Tasmania, causing severe damage to young regeneration stands of *E. regnans*, *E. obliqua*, and *E. delegatensis* and therefore is a pest of major significance.

4. Characters of Tasmanian species of Dicranosternini and Paropsini which feed on *Eucalyptus*

Adults (Figs. 121-160) 6-17 mm long, 4.5-11 mm wide, oval, convex in lateral outline, with greatly expanded prothoracic and elytral margins giving "tortoise"-like appearance. Head (Figs. 6, 7) hypognathous, dorsally punctate, eyes emarginate; antennae filiform; terminal segment of maxillary palps securiform; mandibles cuspidate. Pronotum punctate; anterior angles weakly to strongly mucronate; hind angles broadly rounded. Prosternum (Fig. 7) medianly ridged; propleuron falling steeply away posteriorly to form groove with mesepisternum in which fits fore femur. Mesepimeron reaching coxal cavities; metepisternum with flattened longitudinal groove. Scutellum smooth. Elytra (Fig. 6) covering entire dorsal surface of abdomen; punctate; humeral callus prominent. Epipleuron greatly expanded vertically. Legs (Fig. 8) pubescent, often hidden beneath pronotal and elytral margins. Claws sharply toothed near middle.

Colouring extremely variable; pigments in life often fading to a dull reddish to yellowish brown on death; black pigmentation generally remaining on death; distal segments of antennae, base of head (Figs.16-33),and ventral surface frequently with black pigmentation.

Sexual dimorphism weak to strong; male smaller, less convex, broader, and often darker than female; antennae of male longer; male with proximal tarsal segment of anterior two pairs of legs laterally expanded and rounded (Fig. 8).

Larvae (Figs. 161-192) elongate, eruciform. Frequently tuberculate with tubercles following a distinct pattern on meso-,

metathorax and abdominal segments I-VI (Fig. 9 ). Four larval instars. L1 with black hatching spines on meso-, metathorax and abdominal segment I. Later instars often with reduction or modification of tubercle pattern (Figs. 68-84). Paired, eversible defensive glands on abdominal segment VIII. Larvae frequently brightly coloured and patterned, may form distinct gregarious colonies on foliage of host plant.

Pupae soil-borne, exarate, variably bristled and pubescent, variably and frequently brightly coloured.

Eggs (Figs. 194-221) elongate-oval; chorion sculptured or smooth; with or without external ornamentation; hatching spines of embryo visible prior to eclosion. Deposited singly, or in characteristic rafts or arrangements; often brightly coloured.

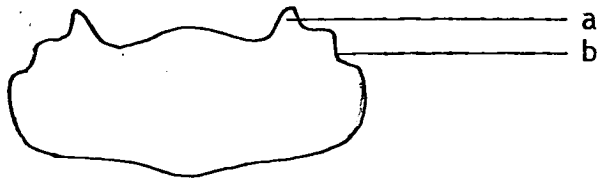



Fig. 3. Pronotum of *Paropsis aegrota*, showing (a) mucronate anterior angle, (b) sinuate margin.

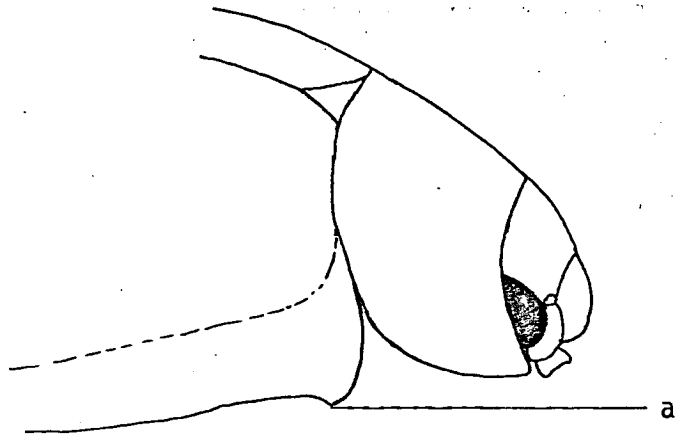



Fig. 4. Side view of anterior portion of *Chrysophtharta* sp. (Ch12), showing (a) mucronate humeral angle of elytron.

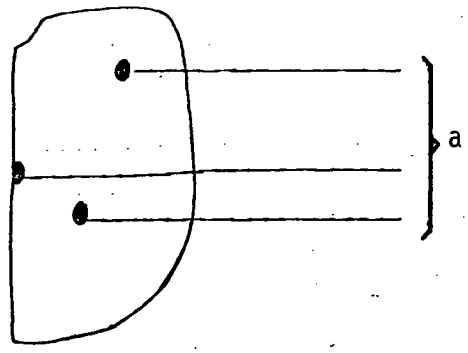



Fig. 5. Elytron of *Paropsis aegrota*, showing (a) positions of most prominent elytral verrucae.

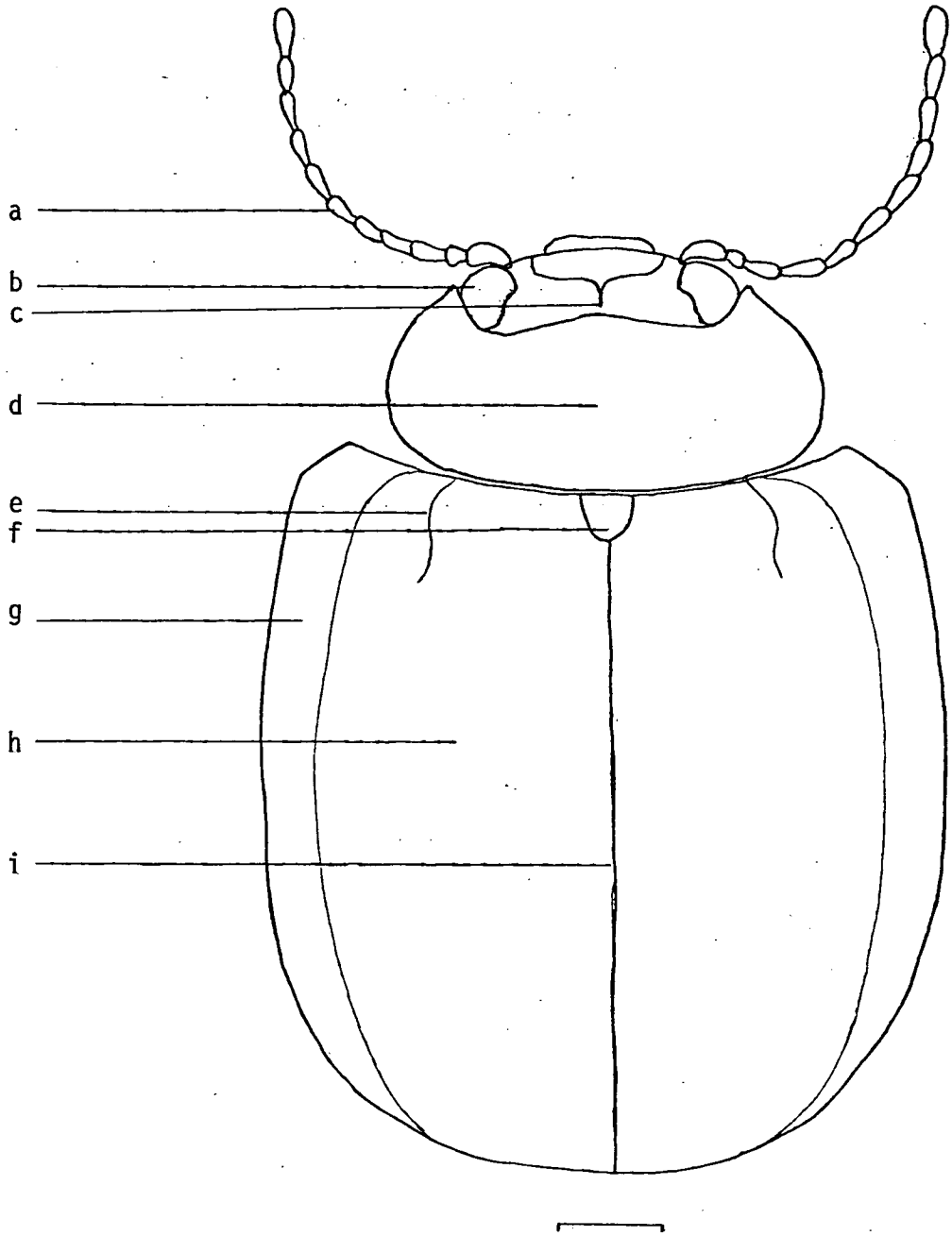



Fig. 6. Dorsal view of *Chrysophtharta bimaculata* showing (a) filiform antenna, (b) emarginate eye, (c) epicranial suture, (d) pronotum, (e) humeral callous, (f) scutellum, (g) elytral margin, (h) elytral disc, (i) elytral suture. (Scale = 1.0 mm)

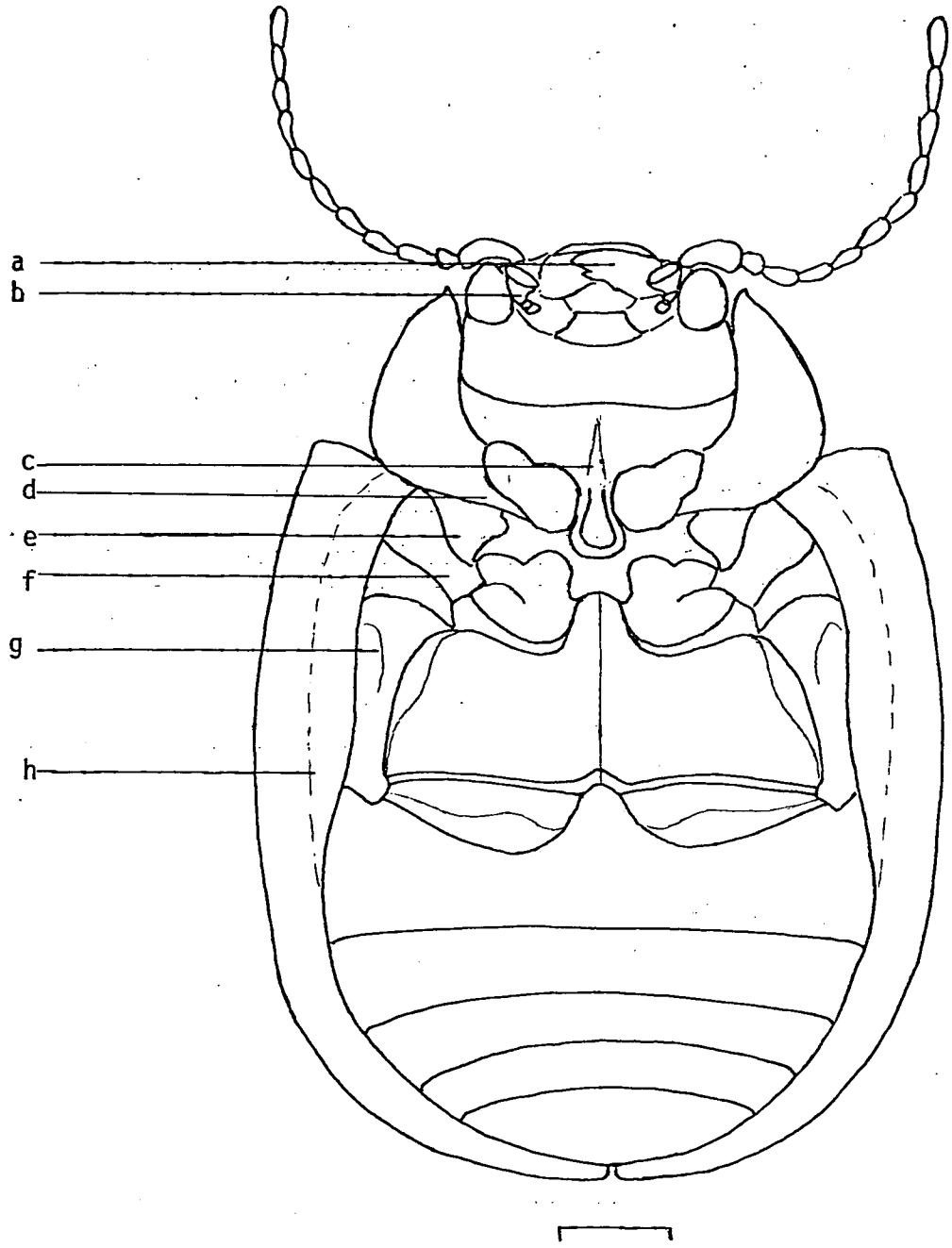



Fig. 7. Ventral view of *Chrysophtharta bimaculata*, showing (a) cuspidate mandibles, (b) securiform maxillary palps, (c) median ridge of prosternum, (d) propleuron, (e) mesepisternum, (f) mesepimeron, (g) metepisternum, (h) epipleuron.

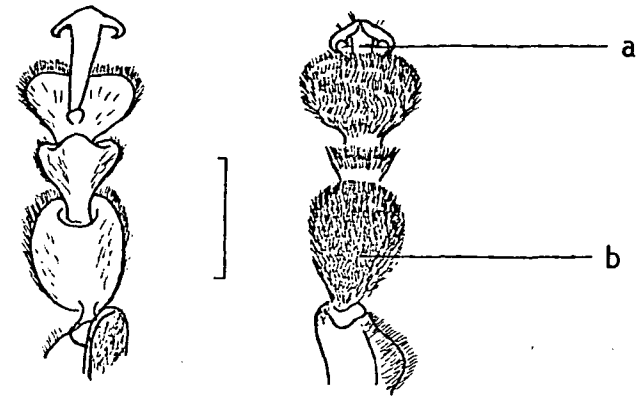



Fig. 8. Dorsal and ventral views of tarsal segments of fore or mid-leg of male *Sterromela trimaculata* showing (a) hooked claw, (b) laterally expanded and rounded proximal segment. (Scale = 1.0 mm)

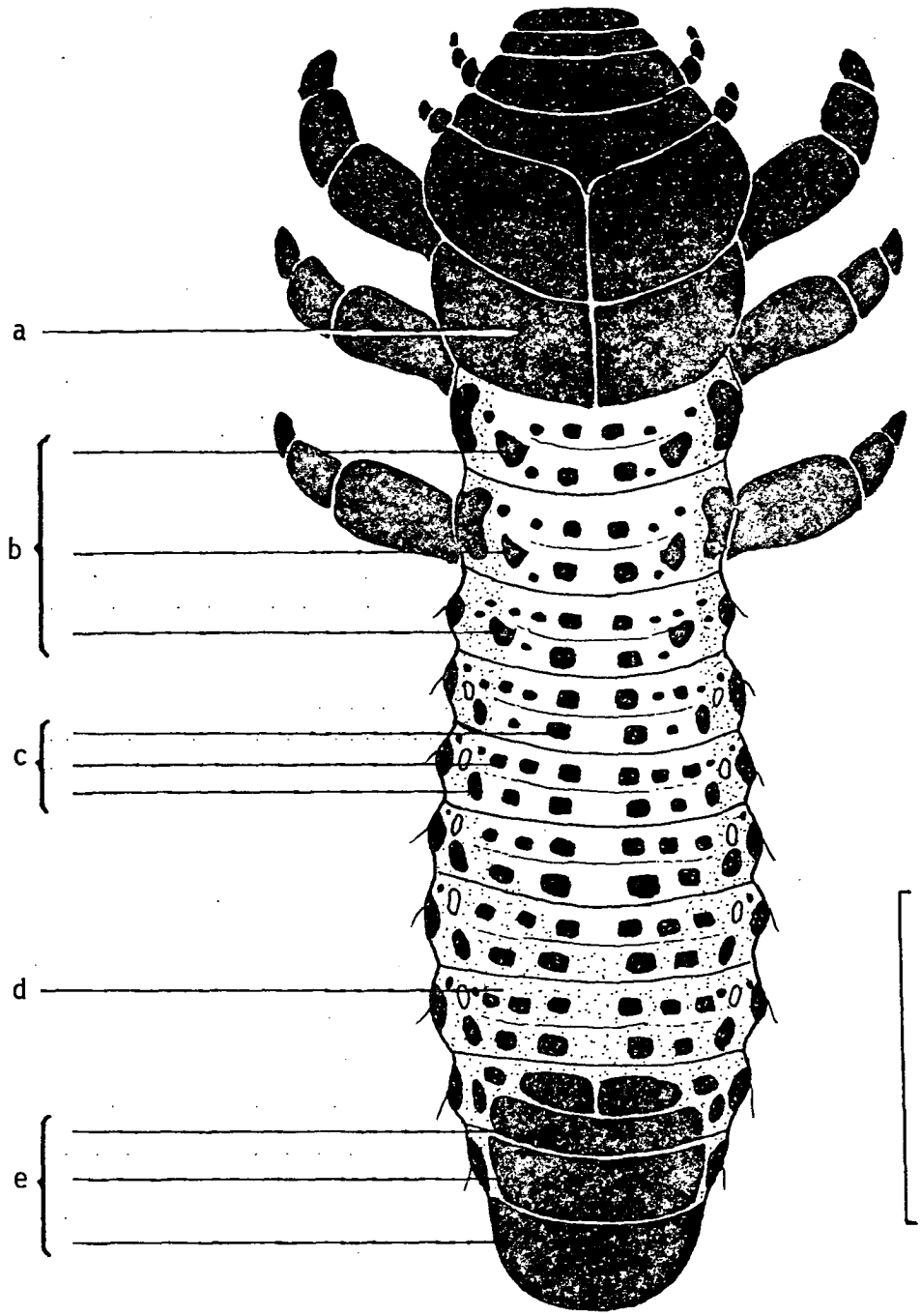



Fig. 9. First instar larva of *Paropsis dilatata* showing (a) black sclerotic protergite, (b) hatching spines, (c) black primary tubercles, (d) minute black secondary tubercles, (e) black sclerites of abdominal tergites VII-IX. (Scale = 1.0 mm)

5. Generic key to adults of Tasmanian *Eucalyptus*-defoliating paropsids

1. Puncturation of disc of elytra non-seriate and often interrupted by the presence of verrucae ..... 2

Puncturation of disc of elytra seriate, in ten rows on each elytron ..... 3

2. Medium to large (9-15 mm long) species; living specimens variably dull-coloured; pronotum with anterior angles mucronate, sides sinuate, or evenly rounded (Fig. 3) ..... *Paropsis* Olivier

Small to medium (6-11 mm long) dark brown species; pronotum normally rounded; living specimens with dorsal surface sometimes covered with white, waxy bloom ..... *Trachymela* Weise

3. Small to medium (6-11 mm long) species; often brightly coloured and sometimes metallic in life; elytral margins widely expanded, often translucent; humeral angles of elytra mucronate (Fig. 4); elytral interstitial puncturation coarse or fine ..... *Chrysophtharta* Weise

Medium to large (8-18 mm long) shining black, brown or yellow-brown species; elytral margins narrowly expanded, opaque; humeral angles of elytra evenly rounded; elytral interstitial puncturation very fine ..... 4

4. Medium to large (8-14 mm long) shining black or brown species; pronotum foveate; epipleuron non-ciliate..... *Paropsisterna* Motschulsky

Large species (11-17 mm long); brown or yellow-brown; sometimes much flattened in lateral outline; pronotum non-foveate; epipleuron ciliate..... *Sterromela* Weise

## 6. Key to fourth instar larvae of Tasmanian *Eucalyptus*-defoliating paropsids

1. Larvae covered with conspicuous setae ..... 2
   Larvae non-setose ..... 4

2. Head capsule entirely black ..... 3
   Head capsule not entirely black ..... *Paropsisterna rufipes* (Pa2)

3. Abdominal segments pale yellow-green ... *Paropsisterna nucea* (Pa1)
   Abdominal segments dark mauve-red ..... *Paropsisterna morio* (Pa3)

4. Protergite entirely black ..... 5
   Protergite not entirely black ..... 10

5. Larvae predominantly black; usually found on foliage during day-time ..... 6
   Meso- and meta-tergites yellowish to greenish; abdominal segments pinkish to reddish mauve; legs long and slender; larvae secretive in habit, usually found under bark during day-time ..... 7

6. Head capsule width about 1.8 mm; sometimes a faint orange lateral stripe from mesotergite to abdominal apex; secondary dorsal tubercles if present, small, sparse; body with uniform width; larvae usually occur on foliage in gregarious colonies..... *Chrysophtharta agricola* (Ch2)

Head capsule width approximately 2.5 mm; secondary dorsal tubercles numerous and well developed; body widest in mid-abdominal region; larvae usually occur singly on foliage ..... *Paropsis porosa* (Ps3)

7. Larvae with well-defined dorsal primary tubercle pattern.....8

Larvae with poorly-defined dorsal primary tubercle pattern, or primary dorsal tubercles absent.....9

8. Head capsule width about 2.2 mm... .....*Trachymela papulosa* (Ta1), *Trachymela* sp. (Ta4)

Head capsule width about 3.0 mm..... *Sterromela lineata* (Sa4)

9. Head capsule width about 3.3 mm..... *Sterromela* sp. (Sa3)

Head capsule width about 1.6 mm.....*Trachymela* sp. (Ta6)

10. Protergite discally black, with orange or brown lateral margin.....11

Protergite not as above.....14

11. Remaining thoracic and abdominal segments uniformly black..... *Paropsis porosa* (Ps3)

Remaining thoracic and abdominal segments black to brown, with variable amounts of orange and sometimes white pigmentation.....12

12. Larvae with white blotches transversely between tubercles..... 13

Larvae without white blotches, but orange pigmentation varying from posterior and lateral tubercles of abdominal segments, to entire abdomen largely orange ..... *Paropsis aegrota* (Ps1)

13. Head capsule width about 3.6 mm; white blotches dorsally in four rows; median orange band from mesotergite to abdominal segment VI.... .....*Paropsis tasmanica* (Ps5)

Head capsule width about 2.8 mm; white blotches in two rows dorsally, and two rows laterally (one on each side); median black band from mesotergite to abdominal segment VI.... .....*Paropsis incarnata* (Ps8)

14. Protergite tuberculate .....15

Protergite not tuberculate .....28

15. Protergite black at margins; finely tuberculate .....16

Protergite not as above .....18

16. Head capsule width about 3.0 mm; primary dorsal tubercles absent on abdominal segments; secondary tubercles strongly developed laterally on meso-, metatergite and abdominal tergites; black regions absent on abdominal segments VII to IX..*Sterromela subcostata* (Sa1)

Head capsule width about 2.0 mm; primary tubercles present dorsally on abdominal segments; secondary tubercles may be present; abdominal segments VII to IX with black regions .....17

17. Abdominal segments with strong development of secondary tubercles dorsally ..... *Trachymela* sp. (Ta8)
Abdominal segments with weak development of secondary body tubercles dorsally ..... *Trachymela* sp. (Ta2)

18. Head capsule completely or mostly black ..... 19
Head capsule not as above ..... 22

19. Head capsule completely black ..... 20
Head capsule mostly black ..... 21

20. Larvae dark olive green; head capsule width about 2.1 mm; larvae usually occur in gregarious groups on foliage ..... *Chrysophtharta bimaculata* (Ch1)
Larvae deep yellow; head capsule width about 2.7 mm; greyish median dorsal band from mesotergite to abdominal segment VI; larvae solilary on foliage ..... *Paropsis charybdis* (Ps4)

21. Head capsule laterally black, with broad median longitudinal yellow-green band; larvae of uniform width; base body colour yellow-green ..... *Chrysophtharta* sp. (Ch13)
Head capsule black laterally and towards base; tuberculate in region of epicranial suture; abdominal segments II to IV much enlarged giving swollen appearance in mid-abdominal region; larvae variable pale to dark brown ..... *Trachymela rugosa* (Ta5)

22. Tubercle pattern of meso-, metathorax and abdominal segments I to VI present, complete.....23

Tubercle pattern not as above.....26

23. Larvae lanceolate with slender tapering abdomen, widest point of larvae at prothorax; head and thoracic segments yellow-green, abdominal segments pink- to mauve-red..... *Chrysophtharta aurea* (Ch3)

Larvae not as above..... 24

24. Larvae short, stout; abdominal segments II to IV much enlarged giving swollen appearance in mid-abdominal region; larvae variable pale to dark brown.....*Trachymela rugosa* (Ta5)

Larvae not as above.....25

25. Larvae pale green, becoming pale pink towards apex of abdomen; sometimes with variable black blotching all over meso-, metathorax and abdominal segments..... *Paropsis dilatata* (Ps6)

Larvae deep yellow, sometimes with a broad, dark greyish dorsal median stripe from mesothorax to abdominal segment VI.....*Paropsis charybdis* (Ps4)

Larvae creamy white to faintly yellow with anterior median tubercle pairs of abdominal segments III to VI greatly enlarged..... *Paropsis* sp. (Ps7)

26. Distal segments of legs mostly yellowish, similar to body colour.....*Chrysophtharta* sp. (Ch11)

Distal segments of legs mostly black.....27

27. Head sparsely tuberculate with black tubercles....
..... *Chrysophtharta decolorata* (Ch4)
Head not as above..... *Chrysophtharta* sp. (Ch12)

28. Head capsule black.....29
Head capsule not black.....30

29. Larvae bright yellow with distinct black median stripe from mesothorax to abdominal segment VI, and black lateral stripes..... *Chrysophtharta variicollis* (Ch7)
Larvae dull green-yellow with dark, greyish lateral stripes.....*Chrysophtharta* sp. (Ch10)

30. Larvae with black lateral tubercles present; poor development of secondary tubercles laterally, colour pale grey-brown.....*Chrysophtharta simsoni* (Ch6)
Larvae not as above.....31

31. Larvae with anterior medio-lateral tubercle pairs of abdominal segments IV to VI prominent, reddish; larvaeyellow to pinkish red.....*Paropsis rubidipes* (Ps2)
Larvae not as above.....32

32. Larvaeuniformly pale, bright green with no dark or black markings.....*Chrysophtharta* sp. (Ch8)
Larvaeyellow.....33

33. Head capsule width about 2.7 mm.....*Chrysophtharta lignea* (Ch9)
Head capsule width about 1.9 mm....*Chrysophtharta nobilitata* (Ch5)

## 7. Genus *Paropsis* Olivier

*Paropsis* Olivier 1807, p. 596; Motschulsky 1860, p. 194; Baly 1864, p. 291 (Section I); Chapuis 1877, p. 67 (Group I); Blackburn 1894, p. 220 (Group I); 1901, p. 160; Weise 1901, p. 165, 166; 1916, p. 155; Selman 1963, p. 43.

*Notoclea* Marsham 1808, p. 284.

### 7.1 Characters of Tasmanian species of *Paropsis*

Adults (Figs.121-129) large (9-15 mm in length); dorsal surface often rugose; elytra with prominent, confused puncturation. Pronotum (Fig. 3) with strongly mucronate anterior angles, and sometimes with sinuous lateral margins. Elytral puncturation evenly distributed or clustered ("acervate" - Blackburn, 1901); when clustered, areas of heavy puncturation tending to form broad bands running from base to apex giving quasi-costate appearance. Puncturation may become dense towards elytral apex giving pitted, quasi-verrucate appearance. Elytra often verrucate (Fig. 5).

Colours in life variable; dorsally dull creamy yellow to yellow-brown, yellow-green or pink, often with greyish, brownish or bluish fascia on elytra.

Larvae (Figs.161-172) tuberculate, at least in early instars (Figs. 68-74 ); sometimes minutely setose in early instars. Later instars with mid-abdominal swelling; tapering posteriorly to a bluntly pointed apex; frequently brightly coloured.

Eggs (Figs. 194-201) with chorion bearing a reticulate pattern; sometimes externally ornamented.

## 7.2 Key to adults of Tasmanian species of *Paropsis*

1. Pronotum with angles more or less mucronate, sides otherwise evenly rounded (or scarcely sinuate).....2

   Pronotum with angles strongly mucronate, sides conspicuously sinuate (Fig. 3 ).....7

2. Undersurface mostly black.....3

   Undersurface entirely yellow-brown, or mostly yellow-brown with limited darker patches.....4

3. Large species (length 12-15 mm); pronotum and elytra strongly verrucate.....*tasmanica* Baly (Ps5)

   Normal sized species (length 10-12 mm); pronotum with obscure dark markings, non-verrucate; elytra weakly verrucate..... *Paropsis* sp. (Ps9)

4. Sides of pronotum slightly sinuate.....5

   Sides of pronotum evenly rounded.....6

5. Highest point of lateral outline about two-thirds of distance from head to elytral apex; disc of pronotum sparsely punctured with dark punctures and without distinct dark maculae; elytra of live specimens pale creamy white with three transverse, broad, dark vittae.....*charybdis* Stål (Ps4)

Highest point of lateral outline at approximately the midpoint of the distance from head to elytral apex; disc of pronotum densely punctured and often with distinct, dark, bilaterally symmetrical maculae; elytra of live specimens pinkish brown to grey sometimes with three faint pale transverse broad vittae..... *dilatata* Erichson (Ps6)

6. Pronotum with anterior angles only slightly mucronate; elytral discal puncturation acervate..... *Paropsis* sp. (Ps7)

Pronotum with anterior angles strongly mucronate; elytral discal puncturation relatively even.... .....*incarnata* Erichson (Ps8)

7. Undersurface mostly or entirely black.....8

Undersurface red-brown..... *rubidipes* Blackburn (Ps2)

8. Elytral puncturation even and uninterrupted; undersurface with yellow blotch on posterior prosternal extremity and broad lateral yellow band running across metasternum and drawn forward medially between coxal cavities of mid legs..... *porosa* Erichson (Ps3)

Elytral puncturation interrupted by conspicuous verrucae (Fig.5 ); undersurface entirely black..... *aegrota* Boisduval (Ps1)

PAROPSIS TASMANICA Baly (Ps5) (Figs. 10, 38, 68, 85, 121, 161, 162, 194)

*Paropsis tasmanica* Baly, 1864, p. 294; Blackburn, 1894, p. 224; 1901, p. 166; Weise, 1916, p. 158.

Occurrence:-

MAKAA: Ridgley, 8.xi.1973, three adults, 15.i.1977, larvae; "Woolnorth" Montagu, 16.xi.1973, one adult; Hastings, 6.i.1977, one adult.

MAKBE: Ridgley, 6.xii.1976, adults; Tiger Ck, 2.ii.1977, two adults.

MAKCA: Ridgley, 6.xii.1976, adults; 15.i.1977, larvae.

MAKHA: Royal George, 2.ii.1977, one larva.

MATEH: Kenzies Hill, 18.i.1977, one larva.

SPEAB: Nubeena, 29.xii.1976, one adult; "The Lea" Hobart, 4.i.1977, five larvae; Badger Head, 13.i.1977, one larva; York Town, 13.i.1977, one larva; Railton, 14.i.1977, one adult, five larvae; Runnymede, 27.i.1977, larvae; Buckland, 27.i.1977, nine adults, larvae; Pipers Brook, 31.i.1977, one adult; Patersonia, 31.i.1977, larvae; Royal George, 2.ii.1977, two adults.

SPIKK: Railton, 14.i.1977, one adult, 15 larvae; Paradise, 18.i.1977, one adult; Buckland, 27.i.1977, seven adults; Pipers Brook, 31.i.1977, one adult; Conroys Gap, 4.i.1974, larvae.

SPINC: Steppes, 8.ii.1977, two adults.

SPINF: Poatina, 18.i.1977, two larvae.

Female

Size 14.55±0.15 x 11.22±0.17 mm (N = 15)

Head finely and closely punctured; unpunctured patch midway between eye and posterior arm of epicranial suture. Pronotum

finely punctured, verrucate; anterior angles strongly mucronate; margins entire. Prosternum with median ridge sulcate. Elytra with puncturation even throughout, interrupted by few to many unpunctured verrucae running in oblique parallel rows from base to apex.

Colour red-brown dorsally, black ventrally. Antennae dark towards apex. Head black at base (Fig. 10) elsewhere with yellow-brown patterning. Lateral margins of pronotum and elytra and elytral verrucae yellow. Yellow-brown patches on legs.

Male

Size 13.41±0.13 x 10.90±0.12 mm (N = 15)

Larva

Head capsule widths L1: 1.2 mm, L2: 1.6 mm, L3: 2.6 mm, L4: 3.6 mm

Maximum length of L4 approximately 20 mm.

L1 dark with complete black tubercle pattern and sclerotic areas; setose.

L2, 3 with prominent white blotches transversely between tubercles (except between median pairs) in posterior row on meso- and metatergite and abdominal tergites.

L4 with dorsal and lateral orange bands; protergite laterally and posteriorly orange.

Egg

Size 2.3 x 0.9 mm

Grey-brown. Chorion with external ornamentation consisting of parallel longitudinal ridges. Cemented longitudinally to leaf edge or petiole end-to-end in chains of 10-30 such that chorion ornamentation is continuous.

Remarks

Baly (1964) described this species from material collected in Tasmania. The present identification is based on his description and Blackburn's (1901) key. The species is distinctly larger than other Tasmanian species of *Paropsis*. Larvae show gregarious colonial behaviour which tends to break up in the fourth (final) instar. Frequently encountered, *P. tasmanica* feeds on a wide range of eucalypts.

PAROPSIS sp. (Ps9) (Figs. 11, 86, 122)

Occurrence:-

MATEH: Rubicon Hills, 23.xi.1977, one adult.

Female

Size 11 x 8 mm (N = 1).

Head finely punctured. Pronotum smooth; disc finely punctured, margins more coarsely punctured. Prosternum with median ridge smooth. Elytral disc smooth, sparsely punctured with large punctures interspersed with small, fine punctures; puncturation more rugose towards margins and apex, becoming quasi-verrucate.

Colour brown dorsally, black ventrally. Head creamy yellow, black at base (Fig.11). Antennae black. Pronotum creamy yellow with obscure brown patterning. Scutellum black. Elytral disc mottled; large punctures dark brown, interstices yellow-brown. Elytral margins creamy yellow.

Remarks

The description of this apparently very rare species is based on one adult female which is the only specimen to far

collected. This female, when maintained in the laboratory, deposited a few mauve-brown eggs which were infertile.

PAROPSIS CHARYBDIS Stål (Ps4) (Figs. 12, 37, 72, 87, 123, 169, 196).

*Notoclea atomaria* Marsham, 1808, p. 286.

*Paropsis atomaria* Boisduval, 1835, p. 562; Baly, 1864, p. 300; Weise, 1901, p. 166.

*Paropsis charybdis* Stål, 1860, p. 466; Blackburn, 1901, p. 162, 164, 178; Selman, 1963, p. 46.

Occurrence:-

SPEAB: Tiger Ck, 9.viii.1973, six adults, 1.i.1974, larvae; Mt. Nicholas, 4.i.1974, one larva; Nubeena, 29.xii.1976, one larva; Carlton R, 30.xii.1976, one adult, two larvae; "The Lea" Hobart, 4.i.1977, larvae; Patersonia, 31.i.1977, two adults.

SPIKK: Ridgley, 15.xii.1973, larvae; Mt. Tor, 23.xi.1974, five adults; Trayheleener Lagoon, 22.xii.1976, ten larvae; Forcett, 28.xii.1977, ten larvae; Roaring Beach, 29.xii.1977, five adults; Coles Bay, 29.i.1977, two adults; Patersonia, 31.i.1977, thirty larvae.

SPINC: "Surrey Hills" 10 km SE of St. Valentines Pk, 26.xii.1974, one adult; Anglers Ck, 28.i.1977, four adults, larvae; Ferrars Tier, 2.ii.1977, one adult; Arthurs Lakes, 8.ii.1977, ten adults.

SPINF: Bothwell, 18.xi.1974, one adult.

Female

Size 11.49±0.13 x 8.56±0.13 mm (N = 16).

Head finely and sparsely punctured. Pronotum with anterior angles weakly mucronate, lateral margins weakly sinuate; disc finely and sparsely punctured. Prosternum with median ridge

sulcate. Elytra with puncturation sparse, weakly acervate at base, rugose at apex.

Colour creamy white dorsally and ventrally. Antennae dark towards apex. Pronotal puncturation dark. Elytral disc patterned with three broad, transverse, brown vittae. Legs and posterior margins of abdominal sternites yellow-brown.

Male

Size 10.49±0.10 x 7.84±0.15 mm (N = 12)

Darker, with more strongly developed elytral discal pattern. Head black at base (Fig. 9).

Larva

Head capsule widths L1: 0.9 mm, L2: 1.3 mm, L3: 2.0 mm, L4: 2.7 mm.

Maximum length of L4 approximately 17 mm.

L1 with complete black tubercle pattern and sclerotic areas.

L2, 3 yellow with tuberculate protergite.

L4 yellow with head capsule and legs variably black or yellow. Abdominal segments VII-IX tuberculate with strong development of median pairs. Dark dorsal band between median tubercle pairs running from base of protergite to abdominal segment VII; lateral dark bands on abdominal segments.

Egg

Size 2.6 x 0.9 mm

Pale yellow. Cemented longitudinally to leaf surface in rafts usually consisting of two or three rows. Number per batch approximately 20-50.

Remarks

This species has been the centre of a taxonomic wrangle involving the names *P. amboinensis* (F.), *P. atomaria*, *P. charybdis*,

and *P. dilatata* Erichson. Selman (1963), in a study of the extant type material designated *P. charybdis* and *P. dilatata* valid species, while *P. amboinensis* was a *nomen dubium*. *P. atomaria* (Marsham) was a synonym of *P. charybdis* due to its preoccupation by *P. atomaria* Olivier, this latter species having been incorrectly identified as *P. reticulata* (Marsham). The species introduced in New Zealand which had been incorrectly identified as *P. dilatata* was correctly identified as *P. charybdis*. The identification of *P. charybdis* found in Tasmania, and based on comparison with preserved specimens from New Zealand, was confirmed by B.J. Selman (*pers. comm.*). Live adults are easily recognized by the characteristic elytral pattern which often fades in preserved material, Larvae do not maintain gregarious colonies, but may be encountered in large numbers. *P. charybdis* is not a common species in Tasmania, but may be locally abundant on *Symphyomyrtus* eucalypts, the preferred hosts.

PAROPSIS DILATATA Erichson (Ps6) (Figs. 9, 13, 39, 71, 88, 124, 171, 172, 197).

*Paropsis dilatata* Erichson, 1842, p. 226; Blackburn, 1894, p. 222, 224; 1901, p. 166, 169, 180; Weise, 1916, p. 156; Selman, 1963, p. 46.

Occurrence:-

MAKAA: Ridgley, 15.i.1977, larvae; Salmon R, 26.xi.1974, adults, larvae; Waterfall Bay, 10.v.1974, adults; Highclere, 23.viii.1974, adults; "Woolnorth" Montagu, 26.xi.1974, five adults.

MAKBE: "Surrey Hills" 7 km W St. Valentines Pk, 27.xii.1974, five adults.

MAKCA: Ridgley, 15.i.1977, larvae, 6.xii.1976, adults; Nicholls Rvt, 3.i.1977, one adult; Florentine Valley, 24.i.1977, one larva.

MATEC: Roaring Beach, 29.xii.1976, two adults.

MATEJ: Mt. Tor, 22.xi.1974, four adults.

SPEAB: Tiger Ck, 1.i.1974, larvae, 1.xii.1974, one adult; Nubeena, 29.xii.1976, one adult.

SPIFL: Ridgley, 16.xii.1977, 15 larvae.

SPINC: Sassafras Hill, 22.xii.1976, one adult; "Surrey Hills" 10 km SE St. Valentines Pk, 21.i.1975, one adult.

Female

Size 12.01±0.12 x 8.54±0.12 mm (N = 15)

Head finely and evenly punctured. Pronotum with anterior angles mucronate, lateral margins weakly sinuate; disc sparsely punctured, rugulose. Elytral puncturation weakly acervate at base, close and rugose at apex.

Colour pinkish brown dorsally, yellow-brown ventrally. Antennae dark towards apex. Pronotum with distinct dark to black bilaterally symmetrical maculae. Elytral disc patterned with three, broad transverse, faint grey vittae.

Male

Size 10.82±0.11 x 8.07±0.12 mm (N = 15).

Head black at base (Fig. 13). Elytral disc steel grey, usually unpatterned. Posterior margin of metasternum, prosternal margins and mesepimeron dark.

Larva

Head capsule widths L1: 1.0 mm, L2: 1.4 mm, L3: 2.1 mm, L4: 2.8 mm.

Maximum length of approximately 17 mm.

L1 dark with complete black tubercle pattern and sclerotic areas (Fig. 105).

L2 with thoracic segments green, abdominal segments red.

L3 with protergite tuberculate.

L4 with head, legs and body green, becoming pink towards abdominal apex. Tubercle pattern faint with strong development of anterior lateral pairs on abdominal segments IV-VI. Variable development of black blotches on meso- and metatergite and abdominal tergites towards prepupal stage, especially on laboratory reared specimens.

Egg

Size 2.8 x 1.0 mm

Pale yellow. Cemented longitudinally to leaf surface adjacent to margin in a raft consisting of a single row. Number per batch approximately 10-40.

Remarks

First described by Erichson (1842), the present identification is based on Blackburn's (1901) key and note, and was confirmed by B.J. Selman (*pers. comm.*). Although closely allied to *P. charybdis*, *P. dilatata* shows stronger sexual dimorphism than any other Tasmanian species of *Paropsis* and the two sexes may not be immediately associated. Larvae are similar in their behaviour to *P. charybdis* larvae. The species is most frequently encountered on Monocalyptus hosts, often in large numbers.

PAROPSIS sp. (Ps7) (Figs. 14, 40, 73, 89, 125, 167, 168, 198).

Occurrence:-

MAKAA: "Woolnorth" Montagu, 12.xi.1975, three adults; Ridgley,

22.xii.1974, one adult; Calder, 28.x.1975, one adult.

MAKBE: "Surrey Hills" 7 km W St. Valentines Pk, 12.xii.1974, two adults.

MAKCA: Tim Shea, 24.i.1977, one adult.

MATEJ: "Surrey Hills" 10 km WSE St. Valentines Pk, 27.xii.1974, one adult.

Female

Size 12.30±0.21 x 9.21±0.12 mm (N = 10).

Head finely but sparsely punctured adjacent to epicranial suture, finely and closely punctured adjacent to eyes, unpunctured space midway between eye and posterior arm of epicranial suture. Pronotum with anterior angles weakly mucronate, lateral margins entire, disc sparsely punctured. Prosternum with median ridge sulcate. Elytra with puncturation strongly acervate at base, at apex very close; rugose-verrucate.

Colour creamy white dorsally, yellow-brown ventrally. Antennae dark towards apex. Head with black markings (Fig. 14 ). Pronotal and discal puncturation grey-brown.

Male

Size 10.64±0.37 x 8.81±0.09 mm (N = 5).

Larva

Head capsule widths L1: 1.4 mm, L2: 1.7 mm, L3: 2.4 mm, L4: 3.0 mm.

Maximum length of approximately 20 mm.

L1 with complete black tubercle pattern and sclerotic areas.

L2 with thoracic segments green, abdominal segments red, protergite tuberculate.

L3 with abdominal segments creamy white, strong development of

median pair of tubercles on anterior sections of abdominal segments III-VI, brown blotch transversely between each pair.

Egg

Size 3.2 x 1.3 mm

Pinkish mauve. Cemented singly or in small, loose groups of up to five at apex of leaf.

Remarks

Adults are easily recognised by the strongly acervate puncturation of the elytra. The larvae are solitary in habit. The species is relatively uncommon, associated mostly with Monocalyptus hosts of the series Obliquae, in the cooler, wetter regions of Tasmania.

PAROPSIS INCARNATA Erichson (Ps8) (Figs. 41, 90, 126, 166, 195).

*Paropsis incarnata* Erichson, 1842, p. 226; Blackburn, 1901, p. 164, 168, 177; Weise, 1916, p. 156.

Occurrence:-

MAKAA: Southport, 26.xii.1973, one adult.

SPEAB: Pipers Brook, 31.i.1977, two adults.

SPIKK: Rubicon Hills, 29.xii.1977, two larvae.

Female

Size 12.5 x 9.0 mm (N = 1).

Head finely and evenly punctured. Pronotum with anterior angles strongly mucronate, lateral margins entire; disc finely, margins more coarsely, punctured, rugulose. Prosternum with median ridge sulcate. Elytra with puncturation at base weakly acervate, at apex close, rugose.

Colour pinkish brown dorsally; yellow-brown ventrally.

Antennae dark towards apex. Head and pronotum yellow-brown with obscure red patterning. Disc of elytra with three, broad, faint grey, transverse bands. Elytral margins yellow-brown.

Male

Size 10.0 x 8.5 mm (N = 1).

Larva

Head capsule widths L1: 0.9 mm, L2: 1.3 mm, L3: 1.9 mm, L4: 2.8 mm.

Maximum length of approximately 15 mm.

L1 with complete black tubercle pattern and sclerotic areas; setose.

L2 mauve-brown; minutely setose.

L3 brown; disc of protergite and median sclerite covering abdominal segments VII-IX shiny black; white patches anteriorly on meso-, and metatergite and abdominal tergites laterally, and between median pairs of tubercles; tubercles with minute setae.

L4 with distinct black lateral stripe extending from abdominal segment I-VI; very faint median stripe.

Egg

Size 2.4 x 0.9 mm

Mauve. Chorion bearing external ornamentation consisting of four longitudinal ridges with hooks projecting at free end of egg. Cemented in a ringed cluster around leaf petiole or shoot.

Remarks

Described by Erichson (1842) from Tasmanian material, this species was considered conspecific with *P. atomaria* Olivier (*P. reticulata* (Marsham)) by Baly (1864), but regarded as a distinct species by Blackburn (1901), on whose key and note the

present identification is based. Eggs and larval stages are morphologically similar to those stages of *P. atomaria* (*P. reticulata*) as described by Cumpston (1939), the major differences being in respect of pigmentation. Further study of variation in mainland Australian populations of *P. atomaria* will be required before the correct status of *P. incarnata* can be determined. It is a rare species in Tasmania.

PAROPSIS RUBIDIPES Blackburn (Ps2) (Figs. 17, 35, 74, 91, 127, 165, 200).

*Paropsis rubidipes* Blackburn, 1901, p. 171, 183; Weise, 1916, p. 158.

Occurrence:-

MAKAA: Rocka Rvt, 1.ii.1974, one adult; Ridgley, 19.i.1976, one adult.

MAKBE: "Surrey Hills" 10 km WSW St. Valentines Pk, 15.xi.1973, adults, larvae.

MAKHA: Arthurs Lakes, 8.ii.1977, two adults.

MATEG: Rocka Rvt, 1.xii.1974, one adult.

MATEJ: "Surrey Hills" 10 km WSW St. Valentines Pk, 15.xii.1973, adults.

MATES: Great Lake, 15.ii.1974, one larva, 18.i.1977, three adults.

SPEAB: Tiger Ck, 18.i.1977, one larva.

SPINC: Arthurs Lakes, 8.ii.1977, two adults, three larvae; Upper Esk, 31.i.1977, one adult; "Surrey Hills" 8 km SE St. Valentines Pk, 18.iv.1975, two adults.

Female

Size 11.79±0.07 x 8.90±0.08 mm (N = 7).

Head finely and evenly punctured. Pronotum with anterior angles strongly mucronate, lateral margins strongly sinuate, disc finely punctured. Prosternum with median ridge sulcate, elytra with puncturation even throughout, interrupted by few to many ill-defined, unpunctured verrucae running in oblique parallel rows from base to apex.

Colour pinkish yellow dorsally; red-brown ventrally. Antennae reddish towards apex. Base of head black (Fig. 17). Obscure red patterning on disc of pronotum. Elytral puncturation dark red. Median ridge of prosternum and mesosternum yellow.

Male

Size 11.01±0.09 x 8.60±0.10 mm (N = 12)

Larva

Head capsule widths, L1: 1.0 mm, L2: 1.6 mm, L3: 2.1 mm, L4: 2.8 mm.

Maximum length of approximately 17 mm.

L1 yellow-green with complete, black tubercle pattern and sclerotic areas; setose.

L2 with protergite tuberculate.

L3 with tubercle pattern faint.

L4 yellow with pinkish colouration developing in prepupal phase. Tubercle pattern lost, with exception of tubercle on either side of anterior median pair on abdominal segments IV-VI which strongly developed, mauve. Black pigmentation of legs and terminal abdominal sclerites lost.

Egg

Size 3.8 x 0.9 mm.

Greenish orange. Cemented at one end to leaf apex or bud; two or three may be cemented end to end.

Remarks

This species was described from Tasmanian material by Blackburn (1901) and the present identification is based on his description. Adults are characterised among other Tasmanian species of *Paropsis* by the red-brown pigmentation of the ventral surface which does not fade on dry preservation. Larvae are solitary in habit, and the species is relatively infrequently encountered.

PAROPSIS POROSA Erichson (Ps3) (Figs. 15, 36, 70, 92, 128, 170, 201).

*Paropsis porosa* Erichson, 1842, p. 226; Baly, 1864, p. 310; Blackburn, 1894, p. 226; 1901, p. 172, 185; Weise, 1916, p. 158.

Occurrence:-

MAKAA: "Woolnorth" Montagu, 6.xi.1974, adults; Ridgley, 15.xi.1973, adults; Poatina, 18.i.1977, two adults; Eddystone Pt, 29.i.1977, one adult; Pipers Brook, 31.i.1977, three adults; Milkshakes Hills, 30.x.1975, adults.

MATEG: Mt. Nelson, 25.ix.1973, one adult.

MATEH: Rubicon Hills, 2.xi.1974, two adults; Barton, 1.xii.1974, two adults.

SPEAB: Tiger Ck, 22.xii.1976, one adult, 1.xii.1974, larvae; York Town, 13.i.1977, 17 adults, larvae; Frankford, 13.i.1977, 17 adults; Salmon R, 17.i.1977, one adult; Smithton, 17.i.1977, one adult; National Park, 24.i.1977, one adult; Tasman Hwy nr Phipps Rd, 27.i.1977, eight adults; Styx Ck Tasman Hwy, 29.i.1977, two adults; Pipers Brook, 31.i.1977, three adults; Blessington, 1.ii.1977, two adults; Upper Esk, 1.ii.1977, two adults.

SPIFL: "Woolnorth" Montagu, 22.xii.1976, adults.

SPIKK: "Summerville" Westbury, 21.i.1977, two adults; Railton, 14.i.1977, 13 adults, two larvae; Myrtle Ck Bass Hwy, 14.i.1977, one adult; Blackwood Ck, 18.i.1977, one adult; Rheban, 28.i.1977, one adult; Lake Leake, 28.i.1977, three adults; Coles Bay, 29.i.1977, eight adults; "Clover Banks" Tasman Hwy, 29.i.1977, four adults; Eddystone Rd, 29.i.1977, 13 adults; Gladstone, 29.i.1977, two adults; Pipers Brook, 31.i.1977, 28 adults; Blessington, 31.i.1977, three adults; Royal George, 2.ii.1977, ten adults.

SPINF: Poatina, 18.i.1977, three adults.

SPINI: "Surrey Hills" 5 km NW Mt Cattley, 15.i.1974, larvae.

Female

Size 9.89±0.07 x 7.14±0.06 mm (N = 13)

Head finely and evenly punctured. Pronotum with anterior angles strongly mucronate, disc finely but evenly punctured. Prosternum with median ridge smooth. Elytra with puncturation even and uninterrupted throughout.

Colour yellow-green to pinkish green dorsally; black ventrally. Antennae and base of head black (Fig. 15). Obscure dark patterning on disc of pronotum. Discal elytral puncturation black. Median ridge of prosternum, mesosternum and a large, angular patch on metasternum, yellow.

Male

Size 9.03±0.08 x 6.90±0.09 mm (N = 15).

Larva

Head capsule widths, L1: 0.08 mm, L2: 1.3 mm, L3: 1.8 mm, L4: 2.5 mm.

Maximum length of approximately 15 mm.

L1, 2, 3 black with complete tubercle pattern and sclerotic areas; L1 setose.

L4 black with lateral margins of prothoracic shield sometimes orange-brown.

Egg

Size 2.3 x 0.8 mm.

Green. Cemented at one end to leaf apex or bud; two or three may be cemented together in an irregular mass.

Remarks

Another species described by Erichson (1842) from Tasmanian material, *P. porosa*, is clearly identified by its relatively small size and the distinct marking in the form of an inverted yellow "Y" on its black ventral surface. The present identification is based on Blackburn's (1901) key, and Baly's (1864) description. *P. porosa* is a common species which does not appear to show a specific preference among its eucalypt hosts and is frequently observed in large numbers on very young seedlings.

PAROPSIS AEGROTA Boisduval (Ps1) (Figs. 3, 5, 16, 34, 69, 93, 129, 163, 164, 199).

*Paropsis aegrota* Boisduval, 1835, p. 563; Blackburn, 1901, p. 170, 183; Cumpston, 1939, p. 364.

Occurrence:-

MAKAA: Salmon R, 26.xi.1974, larvae; "Woolnorth" Montagu, 6.xi.1974, one adult; Gladstone, 29.i.1977, one adult.

MAKBE: "Surrey Hills", 12 km SSW St. Valentines Pk, 7.xii.1973, one adult, 7 km E St. Valentines Pk, 7.xii.1973, one adult, 14.xii.1974, two adults; Florentine Valley, 6 km NNW Wherrett's Lookout, 24.i.1977, three adults.

MAKCA: Ridgley, 8.xi.1973, two adults; Florentine Valley, 3 km NNW Wherrett's Lookout, 24.i.1977, one adult.

MATEC: Tasman Arch, 28.xii.1976, two adults.

MATEG: Mt. Nelson, 15.ix.1973, larvae.

MATEH: Barton, 1.xii.1974, three adults; Gatehouse Marsh, 21.xii.1976, one adult; Ansons Bay, 29.i.1977, one adult.

MATES: Pine Lake, 17.xii.1976, three adults; Swan Bay Great Lake, 19.i.1977, five adults.

SPEAB: Rocka Rvt, 1.xii.1974, adults; Howden, 4.i.1977, 15 larvae; Lady Bay, 6.i.1977, one adult; Tiger Ck, 28.i.1977, one adult; Lilla Villa Bridge Tasman Hwy, 29.i.1977, one adult; Dianas Basin, 29.i.1977, one adult; Pipers Brook, 31.i.1977, seven adults.

SPIKK: Swansea, 22.xii.1976, one adult; Mt. Nelson, 24.xii.1976, one adult; Esperance, 7.i.1977, one adult; Westbury, 12.i.1977, three larvae; Ulverstone, 14.i.1977, one larva, two adults; Paradise, 18.i.1977, one adult; Buckland, 28.i.1877, one larva; Lake Leake, 28.i.1977, one larva; Coles Bay, 29.i.1977, seven adults; St. Marys, 29.i.1977, one adult; Styx Ck Tasman Hwy, 29.i.1977, one adult; Ansons Bay, 29.i.1977, four adults, two larvae; Lwr Turners Marsh, 31.i.1977, one adult; Ridgley, 15.ii.1977, three larvae.

SPINC: Steppes, 17.xii.1976, two adults; Arthurs Lakes, 18.i.1977, two adults.

Female

Size 11.96±0.15 x 8.97±0.11 mm (N = 15).

Head finely and evenly punctured. Pronotum with anterior angles strongly mucronate, lateral margins strongly sinuate, disc finely punctured. Posternum with median ridge sulcate. Elytra

with puncturation even throughout, interrupted by few to many unpunctured verrucae running in oblique parallel rows from base to apex; subhumeral, median and post discal verrucae invariable (Fig. 5).

Colour yellow dorsally; black ventrally. Antennae and base of head black (Fig. 16). Obscure dark patterning on disc of pronotum. Elytral puncturation dark. Legs black with tibiae yellowish towards femora.

Male

Size 11.11±0.15 x 8.54±0.11 mm (N = 15).

Larva

Head capsule widths, L1: 1.0 mm, L2: 1.4 mm, L3: 1.9 mm, L4: 2.7 mm.

Maximum length of approximately 17 mm.

L1, 2 black; tubercle pattern complete; setose.

L3 with lateral margins of prothoracic segment sometimes orange.

L4 colour variable, basically black with more or less orange-brown colouring. Lateral orange blotches on abdominal segments I-VII. Abdominal tergites III-VII with swollen tubercles. At least posterior tubercle two of each segment orange; entire dorsal portion of each segment may be orange giving larva a banded appearance.

Egg

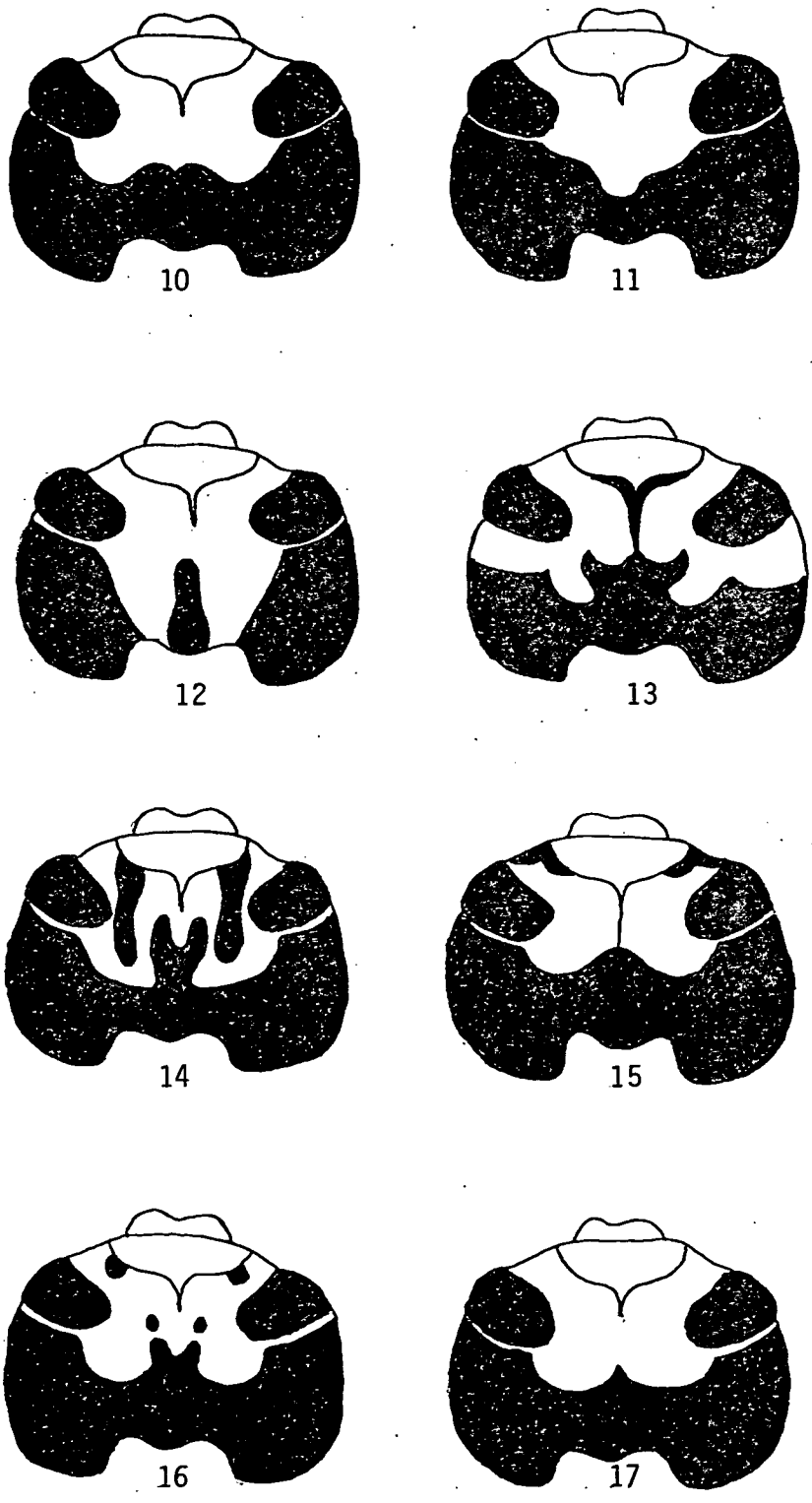
Size 2.9 x 0.9 mm

Pale yellow-green. Cemented by one end of leaf margin in clusters of approximately 10-20.

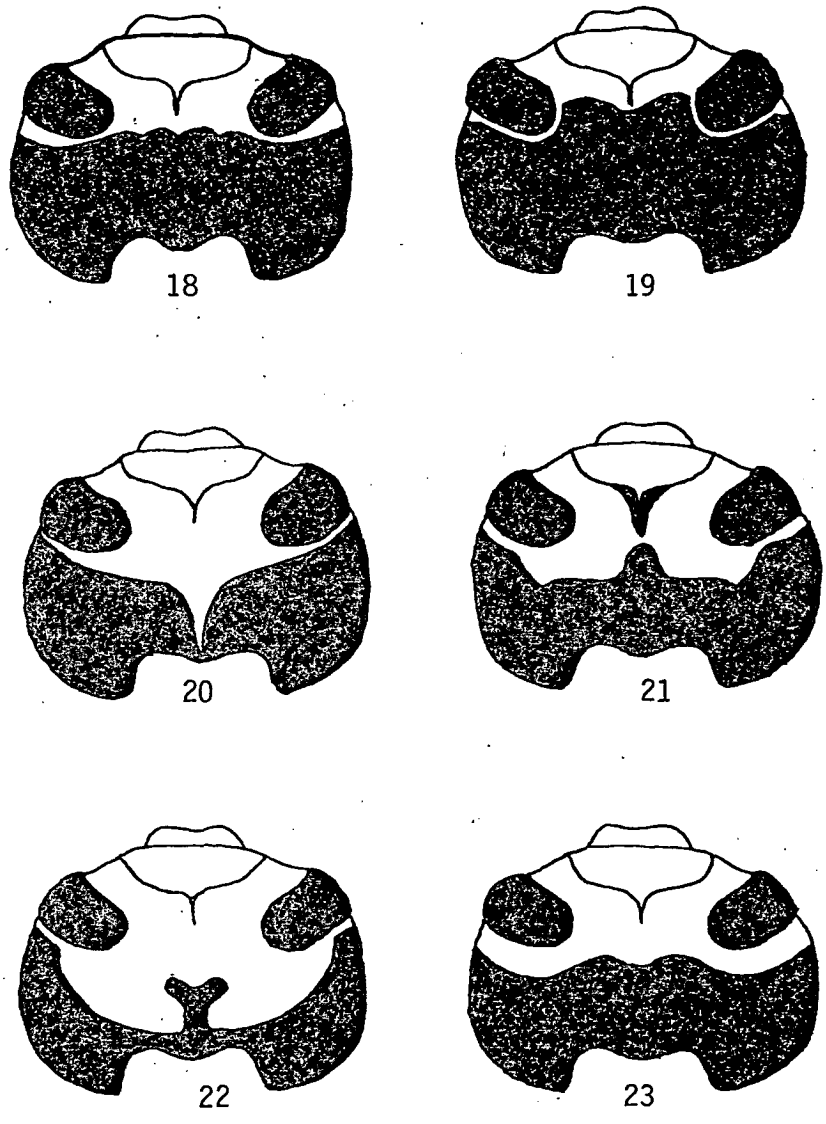
Remarks

Baly (1864) considered this species was possible conspecific with *P. lutea* (Marsham), but Blackburn (1901) regarded the two species as being distinct. The present identification is based on Blackburn's (1901) key and Cumpston's (1939) description of eggs and larvae. In addition to the distinct pigmentation of the larvae, the behavioural pattern of their resting phase clearly identifies this stage of *P. aegrota* in Tasmania. Larvae are normally found in groups of three or four in the angle of a leaf or shoot axil with the tip of the abdomen of the foremost larva resting on the thorax of the larva behind.

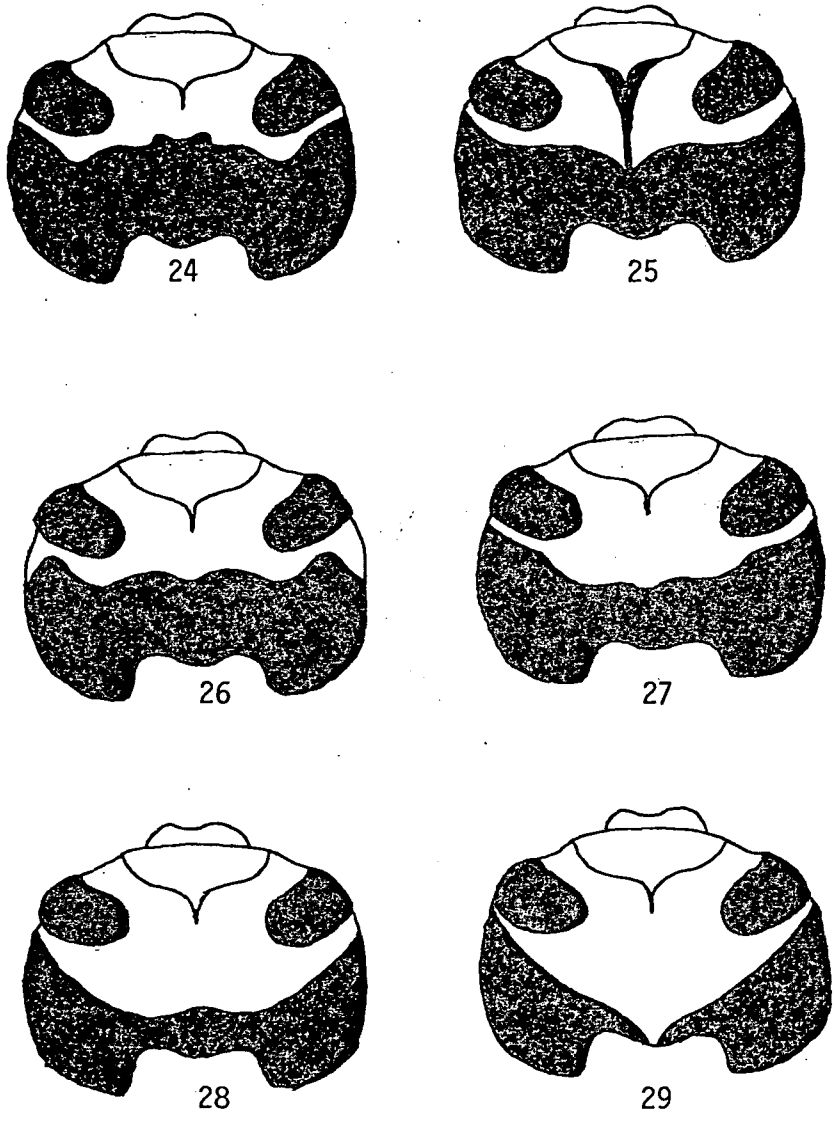
*P. aegrota* is the most commonly encountered and widespread species of *Paropsis* in Tasmania, although it is rarely encountered in large numbers at any locality or on any host eucalypt. Further study of variation among mainland populations will be required before the true status of *P. aegrota* can be established.



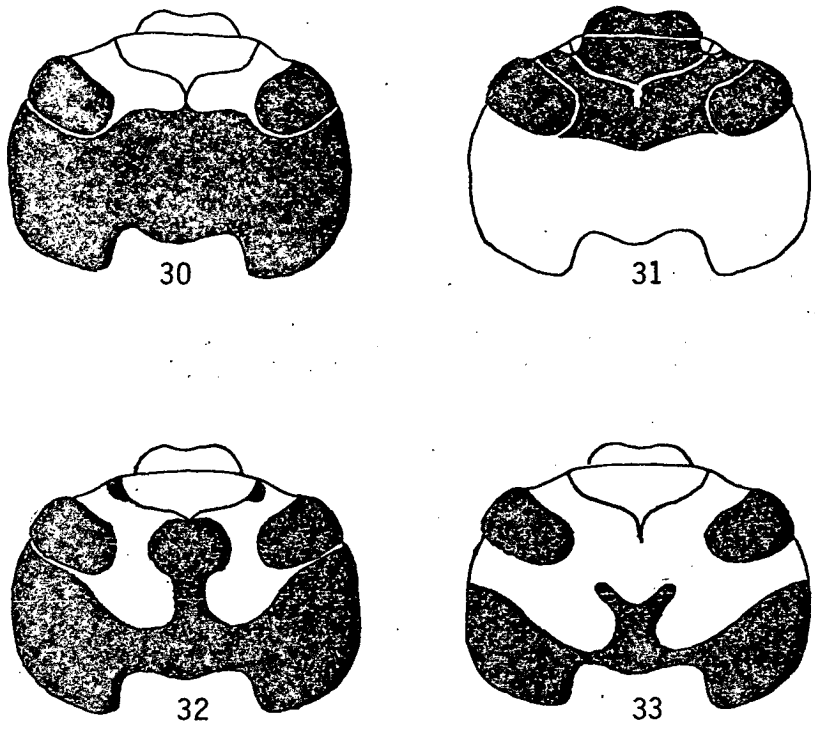

Figs. 10-17. Black pigmentation on dorsal surface of head capsules of (10) *Paropsis tasmanica*, (11) *Paropsis* sp. (Ps9), (12) *P. charybdis*, (13) *P. dilatata*, (14) *Paropsis* sp. (Ps7), (15) *P. porosa*, (16) *P. aegrota*, (17) *P. rubidipes*.




Figs. 18-23. Black pigmentation on dorsal surface of head capsules of: (18) *Chrysophtharta bimaculata*, (19) *C. agricola* (α), (20) *C. aurea*, (21) *C. decolorata*, (22) *C. nobilitata*, (23) *C. simsoni*.




Figs. 24-29. Black pigmentation on dorsal surface of head capsules of: (24) *Chrysophtharta variicollis*, (25) *C. lignea*, (26) *Chrysophtharta* sp. (Ch10), (27) *Chrysophtharta* sp. (Ch11), (28) *Chrysophtharta* sp. (Ch12), (29) *Chrysophtharta* sp. (Ch13).




Figs. 30-33. Black pigmentation on dorsal surface of head capsules of: (30) *Paropsisterna nucea*, (31) *P. rufipes*, (32) *Sterromela trimaculata*, (33) *Sterromela* sp.(Sa3).

## 8. Genus *Trachymela* Weise

*Trachymela* Weise 1908, p. 8; 1916, p. 165.

*Paropsis* Chapuis 1877, p. 87 (Group IV); Blackburn, 1896, p. 637 (Group III, Subgroups I, II, III); 1897, p. 166 (Group III, Subgroup IV).

### 8.1 Characters of Tasmanian species of *Trachymela*

Adults (Figs.130-136) small to medium sized (6 to 11 mm long); normally convex or flattened in lateral outline; dorsal surface often rugose, coated with whitish waxy bloom. Elytral puncturation non-seriate to semi-seriate in approximately 20 rows; puncturation interrupted by elytral verrucae. Elytra sometimes with discal antemedian excavations.

Colour brown.

Larvae (Figs. 173, 174) dull coloured; tuberculate in first three instars at least; body usually elongate, slender, with long, slender legs, but may be short, stout, and distinctly swollen in abdominal region.

Eggs (Figs. 202, 203) with chorion rugose or crenellate.

## 8.2 Key to adults of Tasmanian species of *Trachymela*

1. Species much flattened in lateral outline.....2
   Species normally convex in lateral outline.....3

2. Larger species (about 10 to 11 mm long); pronotum rugosely punctured..... *Trachymela* sp. (Ta7)
   Smaller species (about 7.5 to 9 mm long); pronotum smoothly punctured.....*Trachymela* sp. (Ta2)

3. Elytral puncturation irregular; elytral surface rugose or densely verrucate, with verrucae lighter in colour than surrounding derm; elytral discal antemedian excavations distinct, deeply impressed.....*rugosa* (Chapuis) (Ta5)
   Elytral puncturation more or less regular; elytral surface verrucate but not densely so; verrucae darker in colour than surrounding derm; elytral discal antemedian excavations indistinct and shallow ..... 4

4. Highest point of elytra behind lateral mid-point of body .....*Trachymela* sp. (Ta4)
   Highest point of elytra at or in front of lateral mid-point of body.....5

5. Medium size species (about 7.5 to 9.5 mm long).....6
   Small species (about 5.5 to 7.5 mm long)..... 7

6. Species broadly rounded, sub-circular when viewed from above..... *papulosa* (Chapuis) (Ta1)

   Species narrow, elongate when viewed from above ..... *Trachymela* sp. (Ta8)

7. Small, smooth species (about 5.5 to 6.5 mm long) found on *Eucalyptus rodwayi*..... *Trachymela* sp. (Ta6)

   Larger, more or less rugose species (about 6.5 to 7.5 mm long) found on *Eucalyptus delegatensis* and *E. gunnii* ..... *Trachymela* sp. (Ta3)

TRACHYMELA sp. (Ta7) (Figs. 113,135).

Occurrence:-

MAKAA: Ridgley, 18.ix.1974, two adults.

MAKCA: Ridgley, 22.xi.1976, one adult.

Female

Size 10.64±0.08 x 7.46±0.08 mm (N = 5).

Laterally flattened. Head finely but rugosely punctured. Pronotum densely, rugosely punctured; with a median verruca or longitudinal raised ridge. Elytra coarsely but uniformly punctured, weakly verrucate. Elytral discal antemedian excavations absent.

Colour dark brown, elytral verrucae black.

Male, larva, egg unknown.

Remarks

This rare species agrees most closely with Blackburn's (1907) description of *T. acclivis* (Blackburn) from King Island.

TRACHYMELA sp. (Ta2) (Figs. 43, 114,134).

Occurrence:-

SPIKK: Taroona, 30.ix.1973, seven adults; Ridgley, 1.vi.1974, one adult; 20.viii.1977, one adult.

SPINI: Middlesex Plains, 22.viii.1976, two adults.

Female

Size 8.70±0.13 x 6.15±0.09 mm (N = 12)

Laterally flattened. Head and pronotum finely, somewhat unevenly punctured. Pronotal marginal puncturation not much coarser than discal puncturation. Elytra coarsely but uniformly

punctured; puncturation interrupted by many large, irregularly shaped verrucae. Elytral discal antemedian excavations absent.

Colour dark brown; elytral verrucae black.

Larva

Head capsule widths, L1: 0.6 mm; L2: 1.0 mm; L3: 1.4 mm; L4: 2.0 mm.

Maximum length of approximately 15 mm.

L1, 2, 3 head capsule, legs, prothoracic sclerite and sclerites of abdominal segments VII-IX black. Tubercle pattern complete, black. Thoracic segments pale green; abdominal segments pale brownish-red. L1 minutely setose.

L4 sclerotic areas of head, protergite and abdominal segments VII-IX variable, pale. Tubercles faint, particularly on meso- and metatergite.

Egg

1.7 x 0.6 mm

Pale orange. Deposited in an irregular mass under bark.

Remarks

This species is possibly *T. serpiginosa* (Erichson) (Erichson 1842; Blackburn 1896).

TRACHYMELA RUGOSA (Chapuis) (Ta5) (Figs.46, 115, 130, 173, 202).

*Paropsis rugosa* Chapuis, 1877, p. 91; Blackburn, 1896, p. 645.

*Trachymela rugosa* Weise, 1916, p. 169.

Occurrence:-

MAKAA: "Woolnorth" Montagu, 26.xi.1974, three adults; Salmon R, 26.xi.1974, two adults.

MAKCA: Ridgley, 8.xi.1973, one adult; East Ridgley, 22.xii.1974, one adult.

MAKBE: "Surrey Hills" 4 km W St. Valentines Pk, 14.xii.1974, three adults; Mt. Tor, 23.xi.1974, one adult.

MATEG: Rocka Rvt, 1.xii.1974, one adult.

MATEH: Barton, 1.xii.1974, two adults.

SPEAB: Rocka Rvt, 1.xii.1974, one adult.

SPIKK: Ridgley, 11.xi.1974, one adult.

SPINC: "Surrey Hills", 9 km SE St. Valentines Pk, 22.xi.1974, one adult.

Female

Size 9.63±0.09 x 7.30±0.09 mm (N = 15).

Laterally convex, with highest point of elytra at approximate mid-point of body length. Head and pronotal disc finely punctured; elytral margins very much more coarsely punctured. Elytral discal puncturation very irregular, quasi-costate towards base. Elytral disc rugose; densely verrucate. Elytral discal antemedian excavations prominent, deep.

Colour tan to dark brown. Elytral verrucae paler than surrounding derm.

Male

Size 8.47±0.06 x 6.78±0.11 mm (N = 15).

Larva

Head capsule widths; L1: 1.1 mm, L2: 1.4 mm, L3: 2.0 mm, L4: 2.4 mm.

Maximum length of approximately 12 mm.

L1, 2 head capsule, legs, prothoracic sclerite and sclerites of abdominal segments VII-IX black. Tubercle pattern complete, black; tubercles large, squarish. Thoracic segments pale green; abdominal segments red-brown. Abdomen distinctly swollen in

mid-abdominal region.

L3 protergite tuberculate at base.

L4 brown, stout in abdominal region; epicranial lobes and median portion of protergite black. Mesotergite; metatergite and abdominal segments tuberculate; tubercles large, darker than surrounding derm. Legs pale brown.

Egg

Size 2.3 x 1.0 mm.

Orange-red to brown. Chorion finely reticulate and overlaid with external ornamentation consisting of irregular raised prominences. Deposited on leaf surface in raft consisting of approximately four to eight eggs.

Remarks

Clearly identified by its strongly convex shape and rugose, verrucate elytra in the adult stage. This species was identified from Blackburn's (1896) key, and Chapuis' (1877) description. The adult length of 8 mm given by Chapuis suggests that his description was based on a male specimen.

*T. rugosa* more closely resembles *Paropsis, Chrysophtharta* and *Paropsisterna* spp. in aspects of its life history, than other *Trachymela* spp. Eggs are deposited in a raft on foliage, and larvae feed on foliage during the day-time. Larvae are easily recognised by their swollen abdomens. *T. rugosa* is a common species in the wetter, forested areas of the island.

TRACHYMELA sp. (Ta4) (Figs. 45, 116, 136).

Occurrence:-

MAKBE: "Surrey Hills", 9 km SE St. Valentines Pk, 22.xi.1974, one adult.

MATEJ: "Surrey Hills", 9 km SE St. Valentines Pk, 18.iv.1974, three adults; Mt. Tor, 23.xi.1974, three adults.

MATES: Mt. Tor, 23.xi.1974, five adults.

SPIJA: Cradle Mtn, 18.ii.1977, two adults.

SPINC: "Surrey Hills", 9 km SE St. Valentines Pk, 26.x.1977, one adult.

Female

Size 9.45±0.10 x 7.14±0.13 mm (N = 9).

Laterally convex with highest point of elytra behind mid-point of body length. Head and disc of pronotum finely punctured, pronotal margins more coarsely punctured. Elytral discal puncturation interrupted by semi-costate verrucae which become more discrete towards apex. Elytral discal antemedian excavations faint.

Colour dark brown, with elytral and pronotal margins paler tan. Verrucae black.

Male

Size 8.97±0.10 x 6.68±0.14 mm (N = 11).

Pronotum sometimes with two or more distinct black marks.

Larva

Head capsule widths: L2: 1.2 mm; L3: 1.6 mm; L4 2.2 mm.

Maximum length of L4 approximately 14 mm.

Larvae identical to larvae of Ta1 with exception that in L3, 4 primary tubercles of Ta4 smaller, and secondary tubercles, though present, much less evident.

Remarks

This species closely resembles *T. papulosa* (Erichson) in both the adult and larval stages. It is possibly *T. comma* (Blackburn) (Blackburn 1896).

TRACHYMELA PAPULOSA (Erichson) (Tal) (Figs. 42, 117, 132, 174,203).

*Paropsis papulosa* Erichson, 1842, p. 228; Blackburn, 1897, p. 167.

*Trachymela papulosa* Weise, 1916, p. 168.

Occurrence:-

MAKAA: "Woolnorth" Montagu, 16.xi.1978, one adult.

MATEG: Rocka Rvt, 1.xii.1974, four adults.

MATEH: Steppes, 16.i.1975, one adult.

MATES: Mt. Tor, 23.xi.1974, one adult.

SPEAB: Tiger Ck, 1.xii.1974, seven adults; Bell Bay, 2.xi.1974, one adult.

SPINC: "Surrey Hills" 7 km W St. Valentines Pk, 21.xi.1974, one adult; 9 km SE St. Valentines Pk, 11.i.1975, one adult.

SPINI: "Surrey Hills" 12 km SSE St. Valentines Pk, 1.xii.1974, three adults; 6 km WSW St. Valentines Pk, 20.xi.1974, two adults.

Female

Size 9.10±0.07 x 7.17±0.12 mm (N = 16).

Laterally convex, with highest point of elytra at approximate mid-point of body length. Head finely, evenly punctured. Pronotal disc finely punctured; margins rugosely punctured. Elytra evenly punctured; puncturation interrupted by more or less regular, small, approximately seriate verrucae. Elytral discal antemedian excavations broad and shallow.

Colour pale to dark tan brown; verrucae black.

Male

Size 8.73±0.16 x 6.70±0.12 mm (N = 9).

Pronotum sometimes with two or more distinct black marks.

Larva

Head capsule widths: L1: 0.7 mm; L2: - ; L3: 1.5 mm; L4: 2.2 mm.

Maximum length of L4 approximately 13 mm.

Head capsule, legs, prothoracic sclerite and sclerites of abdominal segments VII-IX black. Tubercle pattern complete, black. Thoracic segments pale green, abdominal segments reddish-mauve.

L1 minutely setose.

L3, 4 with development of minute, black secondary tubercles on thoracic and abdominal segments.

Egg

Size 2.0 x 0.7 mm.

Brown. Chorion crenulate. Deposited in an irregular mass under bark.

Remarks

*T. papulosa* was identified from Erichson's (1842) description and the identification was confirmed by B.J. Selman (*pers. comm.*). The species closely resembles the preceding species *Trachymela* sp. (Ta4), and the following species *Trachymela* sp. (Ta8).

*T. papulosa* is a relatively common and widely distributed species.

TRACHYMELA sp. (Ta8) (Figs. 48, 118, 137).

Occurrence:-

MAKBE: "Surrey Hills", 4 km W St. Valentines Pk, 18.iv.1975, one adult.

SPEAB: Rocka Rvt, 1.xii.1974, two adults.

SPIJA: Mt. Tor, 23.xi.1974, one adult.

SPIKK: Ridgley, 15.ix.1977, one adult.

SPINC: "Surrey Hills", 9 km SE St. Valentines Pk, 11.i.1975, one adult.

SPINI: "Surrey Hills", 12 km SSE St. Valentines Pk, 26.xi.1977, three adults.

Female

Size 8.73±0.11 x 6.39±0.08 mm (N = 9).

Laterally convex, with highest point of elytra at approximate mid-point of body length. Head, pronotal disc, densely, rugosely punctured; pronotal margins coarsely, rugosely punctured. Elytral puncturation interrupted by sparse, small sub-costate verrucae. Elytral discal antemedian excavations broad, shallow.

Colour pale to dark brown, elytral verrucae black.

Male

Size 7.5 x 5.5 mm (N = 1).

Pronotum with irregular black markings.

Larva

Head capsule widths: L1: 0.6 mm; L2: 1.0 mm; L3: 1.4 mm; L4: 2.0 mm.

Maximum length of L4 approximately 11 mm.

Larvae similar in appearance to larvae of *T. papulosa*, L4 with protergite not black but covered with small black tubercles; primary body tubercles faint dorsally; dorsal surface with many small faint secondary tubercles.

Remarks

Adults of this species may be distinguished from *T. papulosa* adults by their distinctly narrower form.

TRACHYMELA sp. (Ta6) (Figs. 47, 119, 133)

Occurrence:-

SPEAH: Tooms Lake, 1.xii.1974, 20 adults; "Surrey Hills, 6 km W St. Valentines Pk, 26.xi.1977, adults, larvae.

Female

Size 6.10±0.15 x 4.76±0.13 mm (N = 8).

Laterally convex with highest point of elytra in front of lateral elytral mid-point. Head and disc of pronotum finely punctured; pronotal margins more coarsely punctured. Elytral discal puncturation interrupted by few to many small verrucae; discal antemedian excavations faintly present, wide, shallow.

Colour brown with black verrucae.

Male

Size 6.09±0.08 x 4.70±0.07 mm (N = 6).

Larva

Head capsule widths: L1: 0.5 mm; L2: 0.8 mm; L3: 1.1 mm; L4: 1.6 mm.

Maximum length of approximately 10 mm.

Head capsule, legs, protergite and tergites of abdominal segments VII-IX black. Tubercles present, black, pattern complete. Thoracic segments pale green, abdominal segments reddish-mauve.

L1, 2 minutely setose.

L3, 4 primary tubercles small, faint; minute secondary tubercles on meso- and metatergite and abdominal tergites.

Egg

Size 1.4 x 0.9 mm.

Bright orange. Deposited in an irregular mass under bark.

Remarks

This small species has only ever been collected from *Eucalyptus rodwayi*.

TRACHYMELA sp. (Ta3) (Figs. 44, 120, 137).

Occurrence:-

MAKBE: "Surrey Hills", 7 km WSW St. Valentines Pk, 18.i.1975, eight adults; 4 km W St. Valentines Pk, 14.xii.1974, three adults; 9 km SE St. Valentines Pk, 14.i.1975, three adults.

SPINI: "Surrey Hills", 12 km SSE St. Valentines Pk, 3.xi.1974, six adults.

Female

Size 7.22±0.10 x 5.79±0.09 mm (N = 15).

Laterally convex with highest point of elytra at approximate mid-point of body length. Head and disc of pronotum finely but rugosely punctured; pronotal margins more coarsely punctured. Elytra rugose; puncturation interrupted by prominent verrucae which are large and irregular near antemedian excavations. Elytral discal antemedian excavations deep, broad.

Colour tan brown; verrucae black.

Male

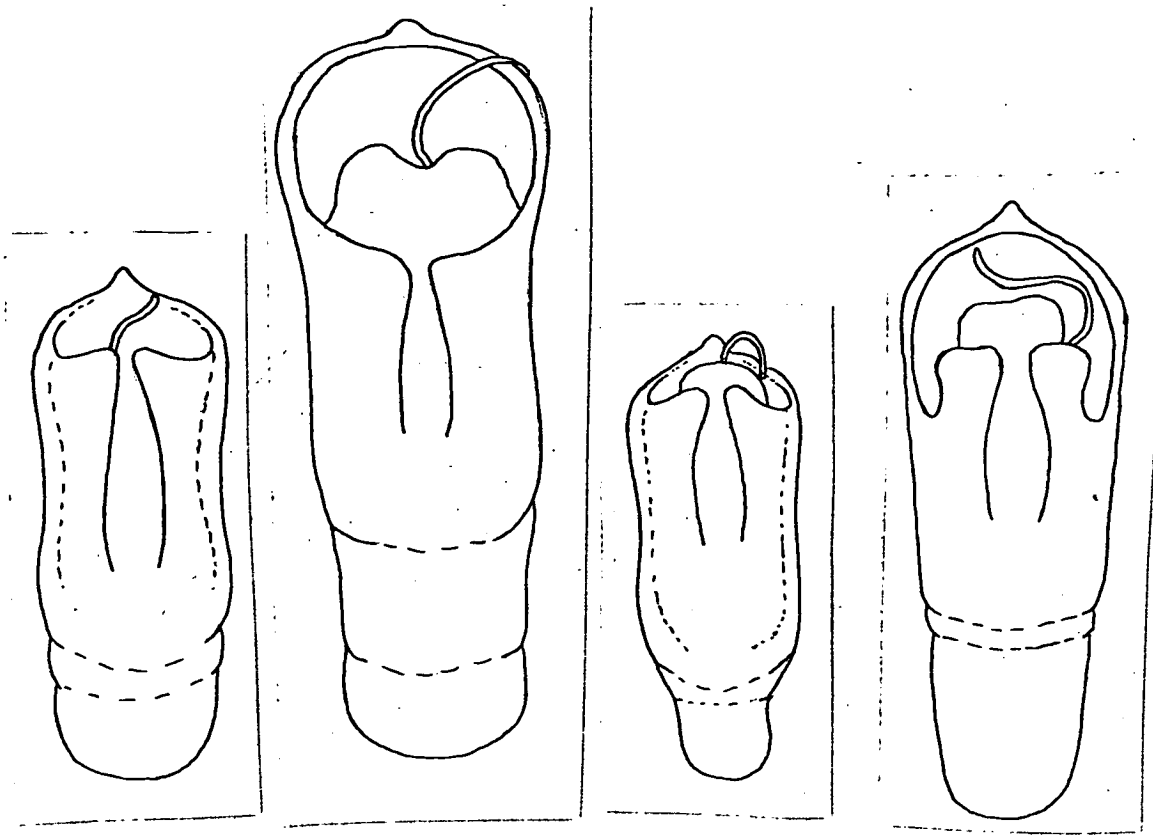
Size 6.72±0.09 x 5.34±0.09 mm (N = 15).

Larva and egg unknown.

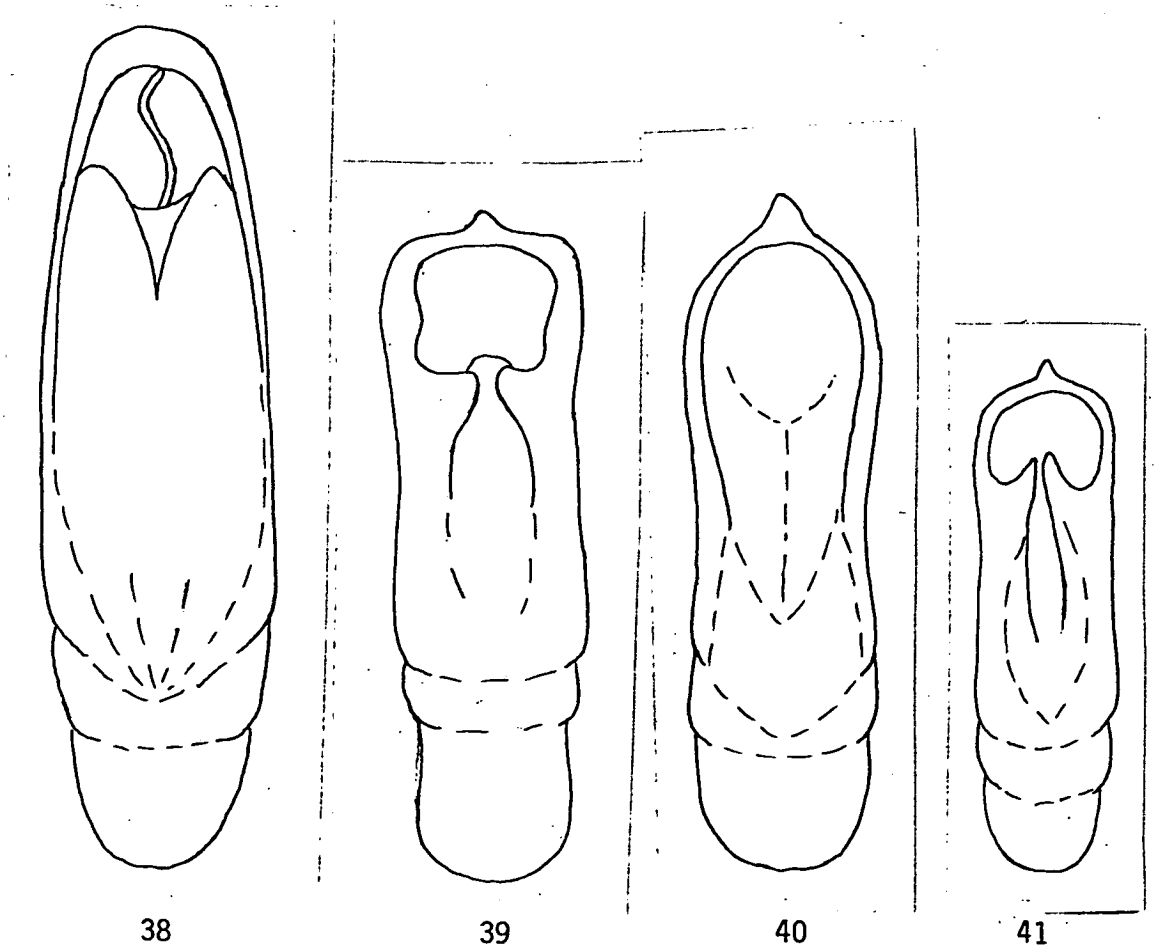
Remarks

Adult beetles of this species are similar in shape to adults of *T. papulosa*, but are smaller and more rugose. In rugosity, this species approaches *T. rugosa* (Chapuis).

Figs. 34-41. Aedeagi of: (34) *Paropsis aegrota*, (35) *P. rubidipes*, (36) *P. porosa*, (37) *P. charybdis*, (38) *P. tasmanica*, (39) *P. dilatata*, (40) *Paropsis* sp. (Ps7), (41) *P. incarnata*.
(Scale = 1.0 mm)

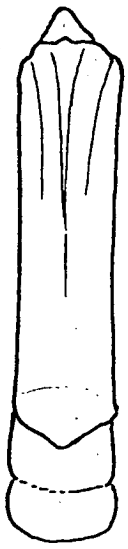


34 35 36 37



38 39 40 41

Figs. 42-48. Aedeagi of: (42) *Trachymela papulosa*, (43) *Trachymela* sp. (Ta2), (44) *Trachymela* sp. (Ta3), (45) *Trachymela* sp. (Ta4), (46) *T. rugosa*, (47) *Trachymela* sp. (Ta6), (48) *Trachymela* sp. (Ta8).
(Scale = 1.0 mm)



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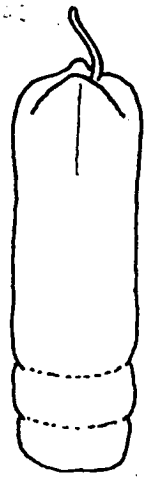

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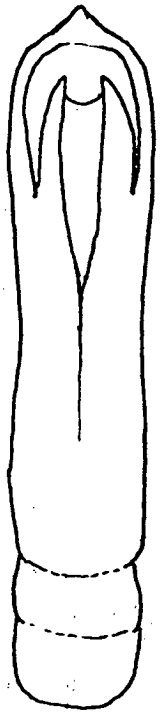

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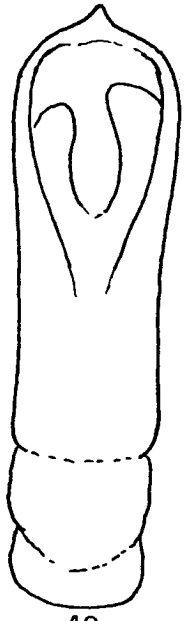

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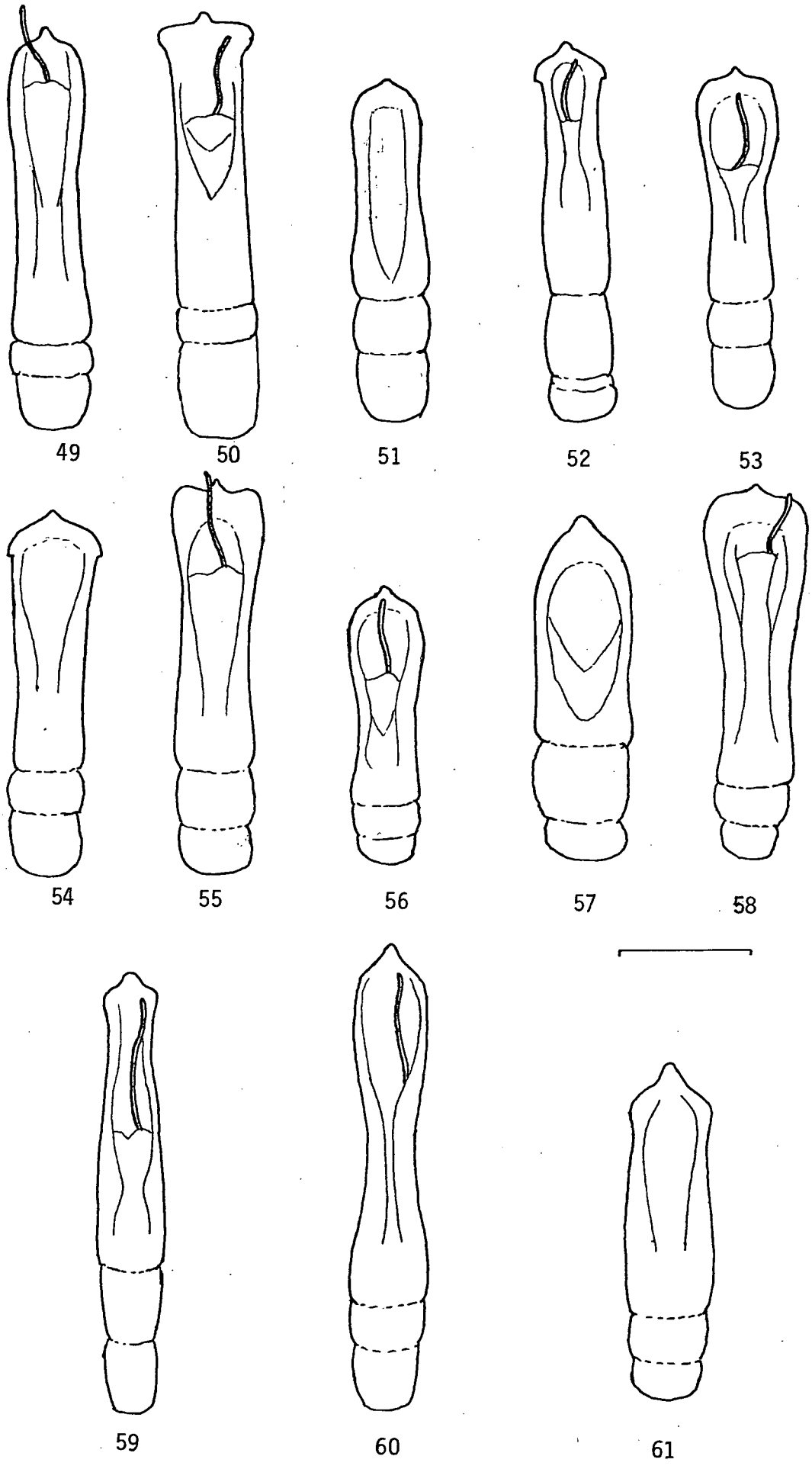
Figs. 49-61. Aedeagi of: (49) *Chrysophtharta bimaculata*, (50) *C. agricola*, (51) *C. aurea*, (52) *C. decolorata*, (53) *C. nobilitata*, (54) *C. simsoni*, (55) *C. variicollis*, (56) *Chrysophtharta* sp. (Ch8), (57) *C. lignea*, (58) *Chrysophtharta* sp. (Ch10), (59) *Chrysophtharta* sp. (Ch11), (60) *Chrysophtharta* sp. (Ch12), (61) *Chrysophtharta* sp. (Ch13).

(Scale = 1.0 mm)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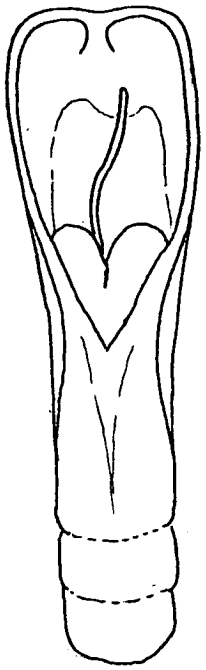
Figs. 62-67. Aedeagi of: (62) *Paropsisterna nucea*, (63) *P. rufipes*, (64) *P. morio*, (65) *Sterromela lineata*, (66) *Sterromela* sp. (Sa3), (67) *S. subcostata*.



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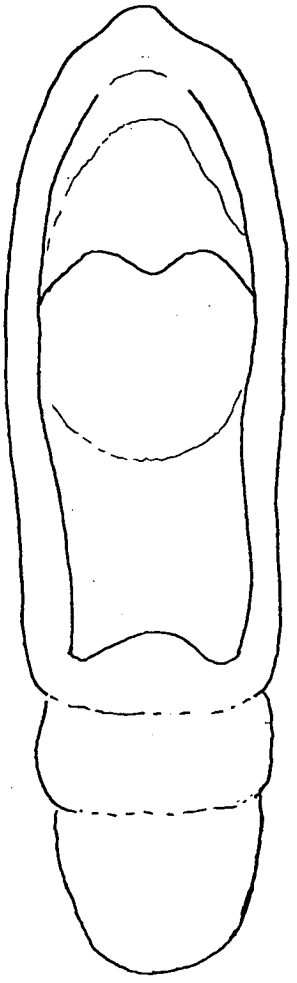

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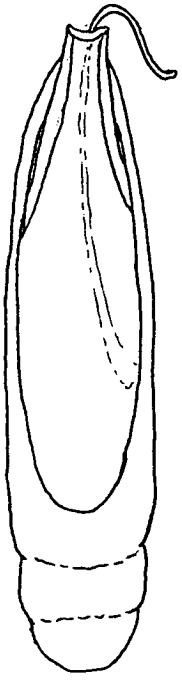

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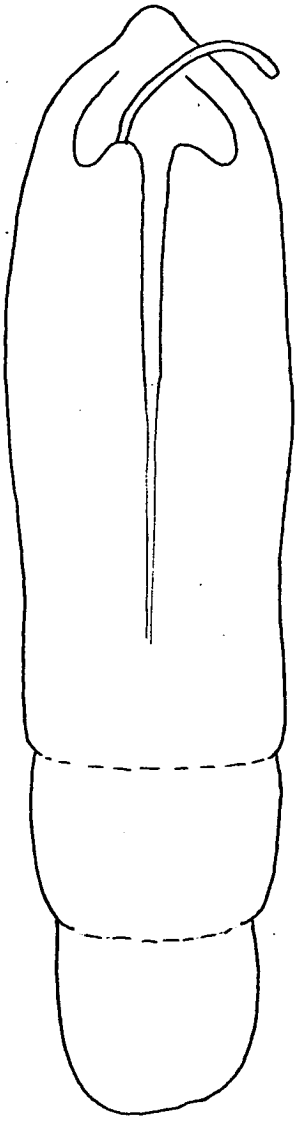

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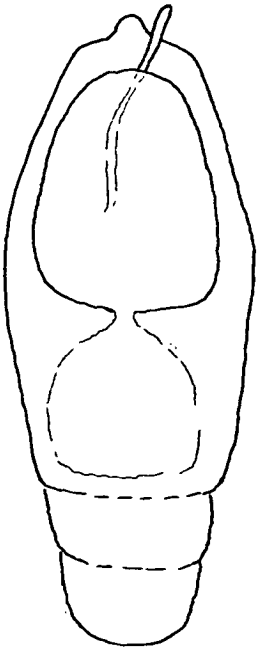

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## 9. Genus *Chrysophtharta* Weise

*Chrysophtharta* Weise, 1901, p. 166; 1916, p. 163.

*Paropsis* Chapuis, 1877, p. 73 (Group III); Blackburn, 1898, p. 255 (Group VI, Subgroup III); 1899, p. 482 (Group VI, Subgroup V).

### 9.1 Characters of Tasmanian species of *Chrysophtharta*

Adults (Figs.138-153), 6.5 to 10 mm long; often brightly coloured, with elytral puncturation seriate in 10 rows. Pronotal margin entire. Elytral seriate puncturation linear and regular or somewhat irregular and sinuous; interstitial puncturation as coarse as, or usually much finer than, seriate puncturation. Humeral angles of elytra mucronate (Fig. 4).

Colours in life variable, elytra often bright, metallic, tesselated; sometimes patterned. Rarely black.

Larvae (Figs. 175-187) similar to larvae of *Paropsis* spp., but may be non-tuberculate in all instars; without pronounced mid-abdominal swelling; non-setose; may be brightly coloured.

Eggs (Figs. 204 - 216) with chorion bearing a tuberculate sculpture.

9.2 Key to adults of Tasmanian species of *Chrysophtharta*

1. Seriate and interstitial puncturation of elytra both coarse and equally coarse..... *lignea* (Erichson) (Ch9)
   Seriate and interstitial puncturation of elytra fine; interstitial puncturation much finer than seriate puncturation..... 2

2. Ventral surface mostly or partly black.....3
   Ventral surface yellow-brown.....9

3. Ventral surface partly black.....4
   Ventral surface mostly black.....5

4. Thoracic sternites black, abdominal sternites yellow-brown with black patches on abdominal sternite I..... *aurea* (Blackburn) (Ch3)
   Prosternum and lateral margins of metasternum, abdominal sternites black; remainder of ventral surface yellow-brown..... *decolorata* (Chapuis) (Ch4)

5. Dorsal surface entirely black with exception of epistome..... *agricola* (Chapuis) (Ch2)
   Dorsal surface not black.....6

6. Pronotum with distinct black maculae..... 7
   Pronotum without distinct black maculae..... *variicollis* (Chapuis) (Ch7)

7. Pronotal maculae consisting of at least two black marks, one on either side of pronotal disc.....8

Pronotal maculae tending to form "U" shape on centre of pronotal disc.....*decolorata* (Chapuis) (Ch4)

8. Pronotal maculae invariably two, one on either side of pronotal disc; species slightly flattened in lateral outline.....*bimaculata* (Olivier) (Ch1)

Pronotal maculae two or four, or maculae confluent on either side of pronotum, or entire pronotum with exception of margins; strongly convex in lateral outline .....*agricola* (Chapuis) (Ch2)

9. Pronotum with two distinct black maculae.... ..... *bimaculata* (Olivier) (Ch1)

Pronotum without black maculae .....10

10. Seriate puncturation of elytra ± linear.....11

Elytral seriate puncturation irregular, two to three punctures may be placed transversely in each row .....*Chrysophtharta* sp. (Ch12)

11. Seriate elytral puncturation linear, fine .....12

Seriate elytral puncturation more or less linear, coarse (but not as coarse as *C. lignea*), giving elytra strongly striate appearance .....16

12. Antennae black from fourth segment to apex.... .....*Chrysophtharta* sp. (Ch13)

Antennae yellow-brown .....13

13. Puncturation of disc of pronotum fine, uniform and dense; smoothly rounded, very convex species.....*aurea* (Blackburn) (Ch3)

Puncturation of disc of pronotum variable.....14

14. Head black at base.....15

Head not black at base.....*Chrysophtharta* sp. (Ch8)

15. Pattern of black pigmentation at base of head as shown in Fig. 22.....*nobilitata* (Erichson) (Ch8)

Pattern of black pigmentation at base of head as shown in Fig. 27.....*Chrysophtharta* sp. (Ch11)

16. Pattern of black pigmentation at base of head as shown in Fig. 21..... *decolorata* (Chapuis) (Ch4)

Pattern of black pigmentation at base of head as shown in Fig. 23.....*simsoni* (Blackburn) (Ch6)

Pattern of black pigmentation at base of head as shown in Fig. 26.....*Chrysophtharta* sp. (Ch10)

CHRYSOPHTHARTA LIGNEA (Erichson) (Ch9) (Figs. 25, 57, 94, 153, 187, 216).

*Paropsis lignea* Erichson, 1842, p. 227; Blackburn, 1898, p. 256, 257.

*Chrysophtharta lignea* Weise, 1916, p. 164.

Occurrence:-

MAKAA: Ridgley, 22.xii.1974, one adult; Salmon R, 17.i.1977, one adult.

MAKBE: "Surrey Hills", 7 km W St. Valentines Pk, 14.xii.1974, four adults, larvae; Snake Ck, Lake Mackenzie Rd, 10.ii.1973, one adult.

MAKCA: Ridgley, 17.i.1975, one adult; Sidling, 26.i.1973, one adult.

MATEJ: "Surrey Hills", 7 km W St. Valentines Pk, 27.xii.1974, one adult.

SPIKK: Ridgley, 11.xi.1974, one adult; Angler Ck, 28.i.1977, one adult.

SPIJA: Mt. Tor, 22.xi.1974, one adult.

SPINC: "Surrey Hills", 10 km SE St. Valentines Pk, 21.i.1975, one adult; Arthurs Lakes, 18.i.1977, two adults.

SPINF: Poatina, 18.i.1977, five adults.

Female

Size 9.84±0.17 x 7.04±0.12 mm (N = 15).

Head and pronotum finely but unevenly punctured, pronotal margins more coarsely punctured. Elytra with seriate puncturation large, linear; interstitial puncturation same size as seriate puncturation.

Colour pale to dark brown. Head black at base (Fig. 25). Pronotum occasionally with three black marks. Disc of elytra sometimes striped, elytral series darker than interstices.

Male

Size 9.17±0.12 x 6.88±0.09 mm (N = 9).

Usually darker than female; disc of pronotum sometimes uniformly dark with pale margin.

Larva

Head capsule widths: L1: 1.2 mm; L2: 1.5 mm; L3: 1.9 mm; L4: 2.7 mm.

Maximum length of L4 approximately 16 mm.

All instars pale yellowish green with thoracic and abdominal segments greyish laterally in L4. Tubercles absent.

Remarks

First described from Tasmanian material by Erichson (1842), *C. lignea* is distinct from all other Tasmanian species of *Chrysophtharta* in its characteristic elytral puncturation.

In Blackburn's (1898) classification, this species is placed in a separate sub-group of Group VI, together with five other mainland Australian species which all have similar elytral puncturation. The present identification is based on Blackburn's key and description.

*C. lignea* is unique among Tasmanian paropsids in its ovoviviparity. It is commonly encountered throughout Tasmania on a wide range of host eucalypt species. Larvae are solitary and never locally abundant.

CHRYSOPHTHARTA AUREA (Blackburn) (Ch3) (Figs. 20, 51, 78, 95, 142, 143, 177, 208).

*Paropsis aurea* Blackburn, 1899, p. 488, 497.

*Chrysophtharta aurea* Weise, 1916, p. 163.

Occurrence:-

MAKAA: Ridgley, 22.xii.1974, four adults; Salmon R, 26.xi.1974, one adult.

MAKBE: Mt. Tor, 23.xi.1974, one adult.

MAKCA: Florentine Valley, 24.i.1977, one adult.

MAKHA: Arthurs Lakes, 8.ii.1977, six adults.

MATEG: Rocka Rvt, 1.xii.1974, six adults.

MATEH: Mt. Barrow, 10.xii.1972, adults; Barton, 1.xii.1974, one adult; Sandford, 22.x.1975, one adult; Golden Valley, 17.xii.1976, one adult; Poatina, 18.i.1977, one adult; Coles Bay, 28.i.1977, six adults; Ansons Bay, 28.i.1977, three adults; Steppes, 16.i.1975, one adult; Bridport, 1.ii.1973, adults.

MATEJ: "Surrey Hills", 10 km SE St. Valentines Pk, 22.ix.1974, adults; 14.i.1975, adults and larvae; Florentine Valley, 24.i.1977, three adults; Mt. Tor, 23.xi.1974, two adults; Hastings, 13.ii.1973, adults.

MATES: Pine Lake, 17.xii.1976, one adult; Hartz Mts, 5.i.1977, one adult; Starvegut Hill, 18.i.1977, 15 adults, larvae.

SPIKK: Penguin, 14.i.1977, one adult.

SPINC: Arthurs Lakes, 18.i.1977, one adult.

Female

Size 8.92±0.10 x 6.51±0.08 mm (N = 15).

Head and pronotum finely and evenly punctured. Elytra with seriate puncturation fine, linear; interstitial puncturation very fine.

Colour of elytral disc of live specimens brilliant, uniform, golden yellow to citrine, sometimes with variable amount of brilliant orange-red colour at base of elytra and adjacent to

suture, but which may cover entire elytral disc. Head, pronotum and elytral margins translucent yellow-brown. Elytral suture black for two-thirds of its distance from scutellum to apex. Ventral surface translucent yellow-brown.

Male

Size 7.65±0.11 x 5.98±0.07 mm (N = 15).

Base of head black (Fig. 20); pro- and mesosternum black; metasternum anteriorly and laterally black. Legs may have black mark on femora.

Larva

Head capsule widths: L1: 0.9 mm; L2: 1.2 mm; L3: 1.5 mm; L4: 2.0 mm.

Maximum length of L4 approximately 15 mm.

Larva with narrow, tapering abdomen in all instars.

L1 with complete black tubercle pattern and sclerotic areas; thoracic segments pale, abdominal segments dark.

L2, 3 with protergite tuberculate; thoracic segments pale green, abdominal segments dark mauve.

L4 with head capsule and protergite yellow, meso- and metatergites yellow-green, abdominal segments pinkish-red; tubercle pattern faint.

Egg

Size 2.8 x 1.1 mm.

Dark mauve-brown.

Remarks

This is a very striking species and easily distinguished by the characteristic larval shape, and brilliant colours in life of the adults. The species was first described from Tasmanian

material, and the present identification is based on Blackburn's (1899) key and original description.

*C. aurea* is most frequently encountered in Monocalyptus hosts of the series Piperitae on which it may occur in large numbers. Larvae are solitary feeders, and their shape may have adaptive significance on the narrow-leaved "peppermints". Adults do not develop orange-red pigmentation until hibernation; in the second season this pigmentation gradually disappears again. Adults from the wetter regions of the island are more citrine in colour, while those from drier regions are more golden yellow.

Although *C. aurea* oviposited profusely in the laboratory, its eggs were never collected in the field.

CHRYSOPHTHARTA DECOLORATA (Chapuis) (Ch4) (Figs. 21, 52, 79, 96, 148, 181, 207).

*Paropsis decolorata* Chapuis, 1877, p. 80; Blackburn, 1899, p. 490, 512.

*Chrysophtharta decolorata* Weise, 1916, p. 164.

Occurrence:-

MAKAA: Ridgley, 19.i.1976, one adult; " Woolnorth" Montagu, 6.xi.1974, one adult.

MAKBE: Derwent Bridge, 4.ii.1973, one adult.

MAKHA: Arthurs Lakes, 8.ii.1977, one adult.

MATEB: Risdon, 22.x.1975, one adult.

MATEG: Tiger Ck, 1.xii.1974, six adults; Mt. Nelson, 10.x.1974, four adults.

MATEH: Rubicon Hills, 2.xi.1974, two adults; Barton, 1.xii.1974, one adult; Bell Bay, 2.xi.1974, one adult; Mt. Barrow, 10.xii.1972,

one adult; Coles Bay, 28.i.1977, one adult; Mathinna, 4.i.1974, adults, larvae; Bridport, 1.ii.1973, adults; Steppes, 19.xii.1972, adults.

MATEC: Bothwell, 18.xi.1974, adults.

MATES: Lake St Clair, 6.i.1974, one adult.

SPEAH: Steppes, 19.xii.1972, adults.

SPEAB: Tolman's Hill, 24.xii.1974, one adult; Howden, 4.i.1977, one adult; Esperance, 7.i.1977, one adult; Maydena, 24.i.1977, two adults.

SPIKK: Taroona, 22.ix.1974, two adults; Rheban, 28.i.1977, three adults; Lake Leake, 28.i.1977, three adults; Coles Bay, 28.i.1977, one adult; Roaring Beach, 29.xii.1977, five adults; Penguin, 14.i.1977, 4 adults, larvae; Smithton, 17.i.1977, one adult.

SPINF: Bothwell, 18.xi.1974, adults, larvae; Poatina, 18.i.1977, one adult.

SPINC: Arthurs Lakes, 8.ii.1977, six adults.

Female

Size 8.26±0.09 x 6.35±0.08 mm (N = 15).

Head and pronotal disc finely but unevenly punctured; margins of pronotum coarsely and rugosely punctured. Elytra with seriate puncturation linear, coarse; interstitial puncturation fine.

Colour of elytral disc of live specimens grey-brown with metallic silver tesselation. Head black at base (Fig. 21). Distal segments of antennae dark. Pronotum dark-brown at margins and with "U" shape centrally on disc. Elytral suture black for two-thirds of its distance from scutellum to apex. Ventral surface translucent yellow-brown.

Male

Size 7.17±0.07 x 5.69±0.08 mm (N = 15).

Darker than female. Prosternum and lateral margins of metasternum and abdominal sternites black.

Larva

Head capsule widths: L1: 0.8 mm, L2: 1.1 mm; L3: 1.4 mm; L4 : 2.1 mm.

Maximum length of approximately 13 mm.

L1 grey; head capsule, legs, sclerites on abdominal segments VII-IX black; black lateral tubercles present.

L2, 3, 4 yellow-grey; head capsule, protergite, and abdominal segments VII-IX with small, black tubercles.

Egg

Size 2.1 x 0.8 mm.

Grey-brown. Cemented longitudinally in a raft consisting of a single row on leaf surface. Number per raft approximately five to eight.

Remarks

This species is most clearly identified by the "U" mark on the pronotum described by Blackburn (1899) on whose key and description the present identification is based.

*C. decolorata* is most commonly encountered on Symphyomyrtus species and species of the series Piperitae (Monocalyptus). Larvae are solitary feeders.

CHRYSOPHTHARTA AGRICOLA (Chapuis) (Ch2) (Figs. 19, 50, 75, 97, 140, 141, 176, 204).

*Paropsis agricola* Chapuis, 1877, p. 75; Blackburn, 1899, p. 487, 491.

*Chrysophtharta agricola* Weise, 1916, p. 163.

Occurrence:-

MAKAA: "Woolnorth" Montagu, 19.x.1976, one adult.

MAKBE: "Surrey Hills", 7 km W St. Valentines Pk, 2.xii.1974, one adult.

SPEAB: Tiger Ck, 1.xii.1974, one adult; Frankford, 13.i.1977, seven adults; Salmon R, 17.i.1977, one adult.

SPIFG: Ridgley, 26.xi.1973, adults and larvae.

SPIFL: "Woolnorth" Montagu, 29.x.1975, four adults; Ridgley, 15.i.1977, adults and larvae.

SPIKK: Ridgely, 22.xii.1974, adults and larvae; Westbury, 12.i.1977, two adults; Penguin, 14.i.1977, two adults; Paradise, 18.i.1977, one adult, larvae.

SPINC: "Surrey Hills" 10 km SE St. Valentines Pk, 22.xi.1974, adults and larvae; Snake Ck, Lake Mackenzie Rd, 12.xii.1972, adults; Arthurs Lakes, 18.i.1977, two adults; Steppes, 16.i.1975, adults and larvae.

SPINF: Bothwell, 18.xi.1974, adults; Poatina, 18.i.1977, two adults.

SPINI: "Surrey Hills", 10 km SSE St. Valentines Pk, 20.xi.1974, adults, larvae.

Female

Size 9.63±0.20 x 7.49±0.14 mm (N = 15).

Head and pronotal disc finely and evenly punctured; pronotal margins coarsely and rugosely punctured. Elytral seriate puncturation irregular, sinuous; interstitial puncturation much finer than seriate puncturation.

Two colour morphs:

α: Elytral disc of live specimens dark grey or red-brown with golden metallic blotches adjacent to scutellum and at humeral callus; elytral disc faintly suffused with golden metallic tesselation. Head black at base (Fig. 19), pronotum with variable black markings usually including two distinct marks, one on either side of pronotal disc. Elytral and pronotal margins translucent yellow-brown or brilliant red. Elytral suture black for approximately one-third distance from scutellum to apex. Ventral surface black.

β: Dorsal surface entirely shining black.

Male

Size 8.86±0.16 x 7.14±0.13 mm (N = 15).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.1 mm; L3: 1.4 mm; L4: 1.8 mm.

Maximum length of approximately 14 mm.

L1, 2, 3 black with complete black tubercle pattern and sclerotic areas.

L4 sometimes faintly orange laterally.

Egg

Size 2.0 x 0.8 mm.

Grey-brown; cemented in an irregular mass of 30 to 60 on leaf surface at apex.

Remarks

*C. agricola* is the only Tasmanian paropsid species with a totally melanic form (β). The original description (Chapuis, 1877) was based on the melanic form, which led to a confusion of

the more common form (α) with *C. bimaculata* (Olivier). The two species are easily distinguished by the lateral form, which is much more convex in *C. agricola* than in *C. bimaculata*. *C. agricola* also has coarser elytral puncturation than *C. bimaculata*. The present identification of *C. agricola* is based on Blackburn's (1899) key and description.

After emergence from pupation adults of both forms are black in their first season, with brilliant red prothoracic and elytral margins. After hibernation, in the second season, the red pigmentation is lost. Form α adults are grey or red-brown with slight golden tesselation while form β adults are entirely black.

Larvae are strongly gregarious, feeding and resting in large groups. *C. agricola* is most frequently encountered on Symphyomyrtus hosts on which large populations may be found. It is common in the wetter regions of the island and is replaced by the closely related species, *C. variicollis*, on Symphyomyrtus hosts in drier regions.

CHRYSOPHTHARTA VARIICOLLIS (Chapuis) (Ch7) (Figs. 24, 55, 83, 98, 144, 179, 205).

*Paropsis variicollis* Chapuis, 1877, p. 82; Blackburn, 1899, p. 487, 490.

*Chrysophtharta variicollis* Weise, 1916, p. 165; Cumpston, 1939, p.360.

Occurrence:-

MAKAA: Geeveston, 6.i.1977, four larvae.

MAKBE: Ridgley, 17.xii.1976, adults and larvae.

MAKCA: Ridgley, 15.iii.1975, one adult.

MATEB: Risdon, 22.x.1975, two adults.

MATEH: Barton, 1.xii.1974, two adults.

MATEC: Tasman Arch, 28.xii.1977, six adults.

SEB:A: "Woolnorth" Montagu, 23.xi.1978, adults.

SPEAB: Tiger Ck, 1.xii.1974, one adult; Tolman's Hill, 24.xii.1976, one adult; Nubeena, 29.xii.1976, 18 adults, larvae; Carlton R, 30.xii.1977, six adults; Howden, 4.i.1977, two adults, larvae; Esperance, 7.i.1977, three adults; York Town, 13.i.1977, one adult, larvae; National Park, 24.i.1977, five adults; Maydena, 24.i.1977, 16 adults; Black Charlies Opening, 27.i.1977, two adults, larvae.

SPIFL: Ridgley, 15.i.1974, adults, larvae; Hastings Caves, 6.i.1977, three adults.

SPIKK: Ridgley, 1.x.1974, two adults; Epping Forest, 3.ii.1974, adults; White Hills, 20.xii.1972, adults, larvae; Taroona, 17.ix.1973, three adults; Buckland, 21.xii.1976, three adults, larvae; Trayheleener Lagoon, 22.xii.1976, three adults, larvae; Mt. Nelson, 24.xii.1976, four adults, larvae; Roaring Beach, 29.xii.1976, eight adults; Exeter, 13.i.1977, one adult, larvae; Smithton, 17.i.1977, adults; Spring Beach, 28.i.1977, six adults; Lake Leake, 28.i.1977, 12 adults, larvae; Coles Bay, 28.i.1977, five adults.

SPINC: "Surrey Hills", 10 km SE St. Valentines Pk, 14.i.1975, one adult; Steppes, 17.xii.1976, one adult; Arthurs Lakes, 18.i.1977, seven adults.

SPINF: Bothwell, 18.xi.1974, adults; Poatina, 18.i.1977, five adults; Maydena, 24.i.1977, adults; Tiger Ck, 1.xii.1974, one adult.

SPINI: Ridgley, 15.i.1974, adults, larvae.

Female

Size 9.13±0.15 x 7.25±0.13 mm (N = 15).

Head finely and evenly punctured. Pronotal disc finely but

unevenly punctured, margins coarsely and rugosely punctured. Elytral seriate puncturation sinuous, irregular; interstitial puncturation fine.

Colour of elytral disc of live specimens orange-brown to yellow-green-brown; tesselated with lighter yellow. Head black at base (Fig. 24). Antennae black distally. Pronotum yellow with brown patterning; elytral margins yellow; scutellum yellow with black margins. Ventral surface and legs black.

Male

Size 8.33±0.17 x 6.83±0.13 mm (N = 15).

Larva

Head capsule widths: L1: 0.7 mm; L2: 1.0 mm; L3: 1.7 mm; L4: 2.3 mm.

Maximum length of approximately 14 mm.

L1 yellow-grey with complete, black tubercle pattern and sclerotic areas.

L2, 3 brilliant yellow with head, legs and sclerotic areas on abdominal segments VII-IX black. Tubercles present but not black.

L4 with very distinct black lateral and dorsal bands from mesothorax to abdominal apex.

Egg

Size 2.0 x 0.7 mm.

Yellow. Cemented in an irregular mass of 30 to 60 eggs on leaf surface.

Remarks

This species is closely related to *C. agricola* from which it is easily distinguished by the dorsal yellow to red-brown colour of the adults, and the bright yellow colour of the larvae.

Adults closely resemble *Chrysophtharta* sp. (Ch13) in dorsal colouring, but may be distinguished from this species by their larger size and black ventral colouring. The present identification is based on Blackburn's (1899) key and description.

Larvae are strongly gregarious, resting and feeding in large groups. The species is extremely common on Symphyomyrtus hosts in dry woodlands.

CHRYSOPHTHARTA BIMACULATA (Olivier)(Ch1) (Figs. 6, 7, 18, 49, 76, 99, 138, 139, 175, 206).

*Paropsis bimaculata* Olivier, 1807, p. 600; Blackburn, 1899, p. 487, 496.

*Chrysophtharta bimaculata* Weise, 1916, p. 163.

Occurrence:-

MAKAA: "Woolnorth" Montagu, 12.xi.1974, adults and larvae; Highclere, 23.viii.1974, adults; Tewkesbury, 26.viii.1974, adults; Ridgley, 16.xii.1975, adults and larvae; Pelverata, 27.ii.1973, one adult; Southport, 9.iii.1973, adults and larvae; Waterfall Bay, 10.v.1974, adults; Calder, 26.x.1975, adults; Arve Valley, 5.i.1977, adults and larvae.

MAKBE: "Surrey Hills", 7 km W St. Valentines Pk, 14.xii.1974, adults and larvae; Lemonthyme, 12.xii.1972, adults; Steppes, 16.i.1975, adults and larvae; Florentine Valley, 24.i.1977, adults and larvae; Ridgley, 15.xii.1975, adults and larvae; Pelion Plains, 1.iii.1973, adults and larvae.

MAKCA: Ridgley, 15.xii.1975, adults and larvae; Florentine Valley, 24.i.1977, adults and larvae; Sidling, 26.i.1973, adults.

MAKHA: Pelion Plains, 1.iii.1973, adults and larvae.

MATEH: Hastings, 13.ii.1973, adults.

MATEJ: "Surrey Hills", 10 km SE St. Valentines Pk, 20.i.1974, adults and larvae.

MATES: Pine Lake, 17.xii.1976, 22 adults.

SPEAB: Nubeena, 29.xii.1976, two adults; Frankford, 13.i.1977, two adults.

SPIJA: Mt. Wellington, 10.iii.1973, one adult.

Female

Size 9.37±0.10 x 6.83±0.11 mm (N = 15).

Head and pronotal disc finely but unevenly punctured; pronotal margins coarsely and rugosely punctured. Elytral seriate puncturation sinuous, somewhat irregular; elytral interstitial puncturation fine.

Colour of elytral disc of living specimens pale green or red-brown with faint gold tesselation. Base of head black, antennae black discally; pronotum and elytral margins translucent yellow-brown; pronotal disc with two distinct black marks. Elytral suture black for approximately one-third its distance from scutellum to apex. Undersurface and legs yellow-brown; sometimes black.

Male

Size 9.05±0.12 x 6.91±0.11 mm (N = 15).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.1 mm; L3: 1.5 mm; L4: 2.1 mm.

Maximum length of approximately 15 mm.

L1 dark with complete black tubercle pattern and sclerotic areas.

L2, 3 dark green with protergite tuberculate.

L4 dark grey-green, with darker lateral and dorsal bands from protergite to abdominal apex.

Egg

Size 2.1 x 0.8 mm.

Grey-brown. Cemented longitudinally in rafts usually of two to three rows on leaf surface. Approximately 15 to 40 eggs per batch.

Remarks

*C. bimaculata* adults are most easily recognised by the two distinct and invariable black marks on the pronotum for which the species is named. The present identification is based on Blackburn's (1899) key and description. Adults in life are variable in colour, changing from pale green to dark red-brown while hibernating. In their second season they change through a brilliant "brick" red to pale green with faint golden tesselation.

Larvae are highly gregarious, forming large colonies. *C. bimaculata* feeds preferentially on Monocalyptus hosts of the series Obliquae. It is extremely common in wet eucalypt forests.

CHRYSOPHTHARTA sp. (Ch12) (Figs. 4, 28, 60, 81, 100, 147, 183, 212).

Occurrence:-

SPEAB: National Park, 24.i.1977, one adult.

SPIKK: Epping forest, 3.ii.1974, one adult; Lake Leake, 28.i.1977, three adults.

SPINF: Bothwell, 18.xi.1974, adults, larvae; Maydena, 24.i.1977, six adults.

Female

Size 8.26±0.14 x 6.27±0.13 mm (N = 15).

Head finely and evenly punctured. Pronotum coarsely and densely punctured, rugose towards margins. Elytral seriate puncturation sinuous and very irregular; interstitial puncturation fine.

Colour of elytral disc of live specimens green; red at base and tesselated with silver-gold; usually two silver-gold blotches adjacent to scutellum, and surrounded with red; red vittae sometimes extending towards elytral apex in region of fifth elytral interstice. Head black at base (Fig. 28). Pronotum translucent yellow-brown with faint markings on disc, red towards margins. Ventral surface translucent yellow-brown.

Male

Size 8.07±0.12 x 6.38±0.08 mm (N = 15).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.2 mm; L3: 1.7 mm; L4: 2.2 mm.

Maximum length of approximately 15 mm.

L1 yellow green; black body tubercles present laterally; dorsally, very faint.

L2 with black tubercles only present on abdominal segments VII and VIII.

L3 with pro- and mesotergite also with black tubercles.

L4 with pro- and mesotergite without black tubercles.

Egg

Size 2.3 x 0.8 mm

Orange. Cemented longitudinally in a raft usually consisting

of a single row of approximately 5 to 20 on leaf surface.

Remarks:

This species closely fits Blackburn's (1899) description of *C. laesa* (Germar), a species widely distributed in Australia. Due to high variability throughout its distribution, B.J. Selman (*pers. comm.*) has suggested that the Tasmanian variant should remain unidentified until further comparisons are possible with mainland forms.

*Chrysophtharta* sp. (Ch12) was only observed in abundance on one occasion, when a large population of adults was encountered feeding and ovipositing on *E. rubida* regrowth, together with *C. agricola, C. variicollis, C. nobilitata* and *C. decolorata* in a cold, dry woodland.

CHRYSOPHTHARTA sp. (Ch13) (Figs. 29, 61, 77, 101, 145, 178, 211).

Occurrence:-

MAKAA: Mt. Nelson, 13.x.1974, one adult.

MATEH: Rubicon, 20.xi.1978, two adults.

SPEAB: Bell Bay, 10.ii.1974, one adult; Bridport, 10.ii.1974, one adult; York Town, 13.i.1977, three adults; Badger Head, 13.i.1977, two adults.

SPIKK: Westbury, 12.i.1977, five adults, larvae; Coles Bay, 28.i.1977, one adult.

SPINF: Bothwell, 18.xi.1974, one adult; Poatina, 18.i.1977, two adults.

Female

Size 7.6 x 6.0 mm (N = 5).

Head and pronotal disc finely and evenly punctured; pronotal margin rugosely punctured. Elytral seriate puncturation linear;

interstitial puncturation fine.

Colour of elytral disc of live specimens pinkish to yellow-brown with faint yellow to pale green tesselations. Head black at base; antennae black distally. Pronotum and elytral margins of live specimens translucent yellow or pale green.

Male

Size 6.9 x 6.0 mm (N = 3).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.1 mm; L3: 1.6 mm; L4: 2.2 mm.

Maximum length of L4 approximately 14 mm.

L1 yellow-green with complete black tubercle pattern and sclerotic areas.

L2, 3 with prothoracic sclerite tuberculate.

L4 with head capsule black laterally, broad yellow-green band in centre.

Egg

Size 2.0 x 0.8 mm.

Yellow-brown. Cemented longitudinally on leaf surface in a raft consisting of a single row of approximately 5-20 eggs

Remarks

This species is possibly *C. obovata* (Chapuis), which is recorded from Tasmania (Chapuis, 1877; Weise, 1916), although descriptions (Chapuis *loc. cit.*; Blackburn, 1899) are not sufficiently adequate to permit unequivocal identification.

Larvae are solitary and the species is relatively uncommon, being encountered most usually in dry woodlands.

CHRYSOPHTHARTA sp. (Ch8) (Figs. 56, 102, 146, 186,209).

Occurrence:-

MAKAA: Ridgley, 14.xi.1973, one adult; "Woolnorth" Montagu, 16.xi.1973, adults.

MAKBE: "Surrey Hills", 7 km W St. Valentines Pk, 30.xi.1975, adults.

MATEJ: "Surrey Hills", 7 km W St. Valentines Pk, 20.xi.1974, adults.

SPEAB: Birralee, 13.i.1977, one adult.

SPIKK: Ridgley, 1.xi.1974, one adult; Paradise, 18.i.1977, one adult.

SPINC: "Surrey Hills", 10 km SE St. Valentines Pk, 14.i.1975, four adults; Arthurs Lakes, 8.ii.1977, one adult.

SPINI: "Surrey Hills", 12 km SSE St. Valentines Pk, 18.i.1975, two adults.

Female

Size 7.86±0.08 x 6.06±0.06 mm (N = 15).

Head and pronotal disc finely and evenly punctured, margins rugosely punctured. Elytral seriate puncturation linear; interstitial puncturation much finer.

Colour of elytral disc of live specimens variably mauve, red, or green with variable yellow tesselation; mauve-red coloration usually deepest towards base of elytra where usually two broad, lateral, mauve vittae. Head pale green in region of epicranial suture, red laterally; pronotum green with red margins; elytral margins and scutellum green. Preserved specimens unformly translucent yellow-brown.

Male

Size 7.36±0.13 x 5.81±0.06 mm (N = 11).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.1 mm; L3: 1.6 mm; L4: 2.0 mm.

Maximum length of approximately 12 mm.

All instars pale green; without tubercles, or black sclerotic areas.

Egg

Size 2.7 x 0.9 mm.

Pale green. Cemented longitudinally in a raft consisting of a single row of approximately 5 to 10 eggs on the leaf surface.

Remarks

This species is unidentifiable from any descriptions.

Larvae are solitary and the species occurs quite frequently in wet forests and sub-alpine woodlands.

CHRYSOPHTHARTA NOBILITATA (Erichson) (Ch5) (Figs. 22, 53, 103, 150, 185, 214).

*Paropsis nobilitata* Erichson, 1842, p. 228; Blackburn, 1899, p. 490, 500.

*Chrysophtharta nobilitata* Weise, 1916, p. 165.

Occurrence:-

MAKAA: "Woolnorth" Montagu, 6.xi.1974, four adults; Ridgley, 15.xii.1973, adults; Salmon R, 17.i.1977, two adults.

MAKBE: "Surrey Hills", 7 km W St. Valentines Pk, 18.i.1975, adults, larvae; Lemonthyme, 12.xii.1972, adults.

MATEG: Mt. Nelson, 10.x.1974, four adults.

MATEH: Bridport, 1.ii.1973, one adult; Bell Bay, 2.xi.1974, two adults; Rubicon Hills, 2.xi.1974, three adults; Barton, 1.xii.1974, two adults; Priory, Ansons Bay Rd, 28.i.1977, nine adults.

MATEJ: "Surrey Hills", 10 km SE St. Valentines Pk, 21.i.1975, five adults; "Surrey Hills", 7 km W St. Valentines Pk, 21.xii.1975, six adults.

SPEAB: Royal George, 7.ix.1974, one adult; Nubeena, 29.xii.1977, two adults; Carlton R, 30.xii.1977, one adult; Esperance, 7.i.1977, two adults; York Town, 13.i.1977, one adult; Birralee, 13.i.1977, one adult; National Park, 24.i.1977, two adults; Maydena, 24.i.1977, two adults.

SPIKK: Taroona, 17.ix.1973, one adult; Mt. Nelson, 4.x.1973, adults; Forcett, 28.xii.1977, one adult; Roaring Beach, 29.xii.1977, two adults; Exeter, 13.i.1977, two adults; Penguin, 14.i.1977, four adults; Spring Beach, 28.i.1977, two adults; Smithton, 17.i.1977, four adults; Ridgley, 11.xi.1974, one adult.

SPINC: "Surrey Hills", 10 km SE St. Valentines Pk, 22.xi.1974, two adults.

SPINF: Bothwell, 18.xi.1974, adults; Poatina, 18.i.1977, one adult; Tiger Ck, 1.xii.1974, two adults.

SPINI: "Surrey Hills", 12 km SSE St. Valentines Pk, 3.xi.1974, three adults.

Female

Size 7.33±0.10 x 5.90±0.10 mm (N = 15).

Head and pronotal disc finely but unevenly punctured, pronotal margins rugosely punctured. Elytral seriate puncturation linear; interstitial puncturation finer than elytral puncturation.

Colour of elytral disc of live specimens patterned red, black

and metallic golden. Elytral disc predominantly brilliant red with four distinct gold blotches; two at base, adjacent to scutellum, and two adjacent to suture, two-thirds of its distance from scutellum to apex; golden blotches variably edged with black; posterior pair faintly expanded in wide arc towards elytral apex; elytral disc sub-marginally golden edged on its inner border with red portion with sinuous black vitta; red portion of elytra with faint silver-gold tesselations; elytral suture black for approximately one-third of its distance from scutellum to apex. Head black at base; pronotum translucent yellow-brown with red colouring towards margins; elytral margins translucent yellow-brown.

Male

Size 6.85±0.11 x 5.53±0.09 mm (N = 15).

Larva

Head capsule widths: L1: 0.7 mm; L2: 1.0 mm; L3: 1.4 mm; L4: 1.9 mm.

Maximum length of approximately 12 mm.

Larvae pale yellow in all instars; without tubercles or black sclerotic areas.

Egg

Size 2.0 x 0.7 mm.

Pale yellow. Cemented longitudinally in a raft consisting of a single row of approximately 4 to 8 eggs on leaf surface.

Remarks

First described from Tasmanian material by Erichson (1842), the present identification of *C. nobilitata* is based on Blackburn's (1899) key and description. Live adults are easily recognised by the characteristic elytral pattern.

Larvae are solitary. The species is very common on a wide range of hosts in many localities.

CHRYSOPHTHARTA sp. (Ch11) (Figs. 27, 59, 80, 104, 149, 182, 213).

Occurrence:-

MATEH: Barton, 1.xii.1974, six adults; Rubicon Hills, 23.xi.1977, one adult.

SPIKK: Exeter, 13.i.1977, two adults.

Female

Size 8.5 x 6.4 mm (N = 3).

Head and pronotal disc finely and evenly punctured; pronotal margins rugosely punctured. Elytral seriate puncturation linear; interstitial puncturation finer than seriate puncturation.

Colour of elytral disc of live specimens reddish-mauve with three broad fascia; one at base, one at elytral mid-point, and one at apex; consisting of dense silver-gold tesselations; middle fascia laterally expanded anteriorly and posteriorly. Head black at base; red in region of epicranial suture; pronotum covered with reddish markings; elytral margins translucent yellow-brown, suture black for one-third of its distance from base towards apex.

Male

Size 7.4 x 6.0 mm (N = 3).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.1 mm; L3: 1.5 mm; L4: 2.0 mm.

Maximum length of approximately 14 mm.

L1 yellow, with head, legs, abdominal sclerites VII-IX and lateral margins of prothoracic shield black; black body tubercles present and complete.

L2, 3, 4 without black sclerotic areas and usual body tubercles; head capsule, prothoracic shield and abdominal sclerites VII-IX tuberculate. All segments with faint lateral tubercles.

Egg

Size 2.0 x 0.8 mm.

Bright yellow. Cemented longitudinally in a raft consisting of a single row of approximately 15 - 30 on leaf surface.

Remarks

This species is unidentifiable from any descriptions. Live adults are easily recognised by the characteristic elytral pattern.

Larvae are solitary. The species is rare.

CHRYSOPHTHARTA SIMSONI (Blackburn) (Ch6) (Figs. 23, 54, 82, 105, 152, 184, 210).

*Paropsis simsoni* Blackburn, 1899, p. 488, 501.

*Chrysophtharta simsoni* Weise, 1916, p. 165.

Occurrence:-

MAKBE: "Surrey Hills", 7 km W St. Valentines Pk, 14.xii.1974, five adults; 29.i.1975, one adult; 13.ii.1975, one adult; 20.iii.1975, one adult; 18.iv.1975, two adults; "Surrey Hills", 10 km SE St. Valentines Pk, 21.i.1975, one adult.

SPINC: "Surrey Hills", 10 km SE St. Valentines Pk, 12.i.1977, one adult.

Female

Size 8.55±0.16 x 6.61±0.09 mm (N = 9).

Head densely punctured; pronotum coarsely and rugosely punctured. Seriate puncturation mostly linear but sometimes irregular; interstitial puncturation finer than seriate puncturation.

Colour of elytral disc of live specimens variable greenish-golden to dark orange-red, often with dark brownish-black elytral fascia drawn both forwards and backwards laterally in approximate "H" shape with cross-bar crossing elytral suture one-third of its distance from base to apex; elytra variable tesselated with metallic silver-gold. Base of head, scutellum, and elytral suture black for one-third to two-thirds of the distance from base to apex. Antennae variably black towards apices.

Male

Size 7.81±0.08 x 6.48±0.08 mm (N = 6).

Sometimes redder than female.

Larva

Head capsule widths: L3: 1.7 mm; L4: 2.1 mm.

Maximum length of approximately 14 mm.

L3 pale grey-brown with legs black and lateral black body tubercles only present.

L4 with black of legs largely lost.

Egg

Size 2.5 x 0.9 mm.

Colour white to orange-pink. Cemented longitudinally in a raft consisting of a single row of approximately 5-10 eggs on leaf surface.

Remarks

Adults of *C. simsoni* most closely resemble *C. aurea* in their live colours. However, they may be distinguished from the latter species by the darker pinkish-green to pinkish-orange colour of the elytra, the smaller size and the more rugose elytral puncturation. The present identification was based on Blackburn's (1899) key and description, and confirmed by B.J. Selman (*pers. comm.*).

Larvae are solitary. The species is quite rare and is known only from wet, highland forests.

CHRYSOPHTHARTA sp. (Ch10) (Figs. 26, 58, 84, 106, 151, 180, 215).

Occurrence:-

MATEH: Priory Ansons Bay Rd, 28.i.1977, four adults; Coles Bay, 28.i.1977, one adult.

SPEAB: Rocka Rvt, 1.xii.1974, three adults, larvae; National Park, 24.i.1977, six adults; Maydena, 24.i.1977, one adult; Black Charlies Opening, 27.i.1977.

SPIKK: "Surrey Hills", 10 km SE St. Valentines Pk, 3.i.1975, three adults; Arthurs Lakes, 18.i.1977, one adult.

SPINF: Maydena, 24.i.1977, two adults.

SPINI: "Surrey Hills", 12 km SSE St. Valentines Pk, 20.xii.1973, one adult.

Female

Size 8.28±0.15 x 6.24±0.07 mm (N = 7).

Head finely but unevenly punctured, pronotum coarsely and rugosely punctured. Elytra with seriate puncturation, slightly irregular, sinuous; interstitial elytral puncturation much finer than seriate puncturation.

Colour of elytral disc of live specimens dark greenish to reddish-black, with faint lighter yellowish tesselation. Two distinct yellowish blotches at base of elytra, adjacent to scutellum; yellowish vittae arising sub-suturally just posterior to mid-point and directed obliquely posteriorly laterally to fifth elytral interstice thence inward to elytral apex, forming diamond-shaped figure on both elytra; sub-marginal reddish to yellowish vittae on each elytron extending from base to apex. Base of head black, pronotum, translucent yellow-brown, sometimes with obscure dark markings; elytral margins translucent yellow-brown.

Male

Size 8.1 x 6.2 mm (N = 2).

Often redder than female.

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.2 mm; L3: 1.5 mm; L4: 2.1 mm.

Maximum length of approximately 13 mm.

L1 yellow-green with legs, head and sclerites of abdominal segments VII-IX black. Tubercles present laterally, black.

L2, 3 with protergite black laterally.

L4 with dark lateral stripe from protergite to abdominal apex.

Egg

Size 1.9 x 0.8 mm.

Colour yellow-green. Cemented longitudinally in a raft consisting of a single row of approximately 5 to 10 eggs on leaf surface.

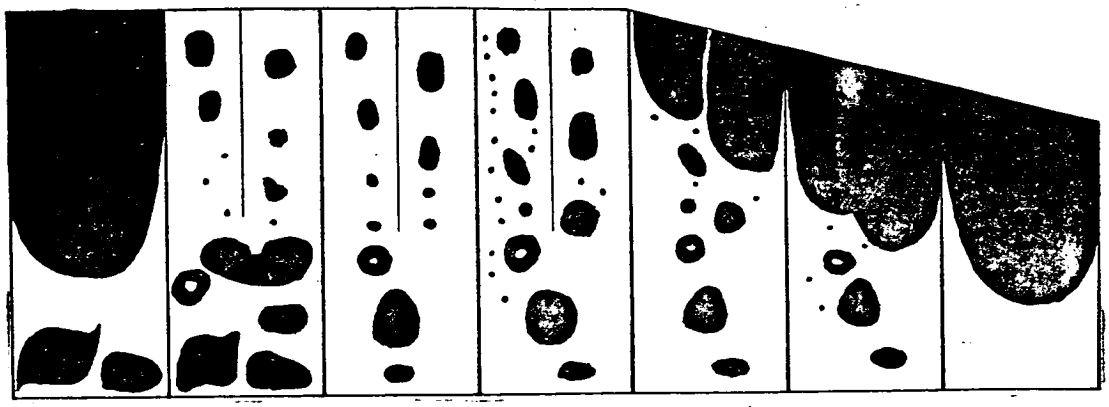
Remarks

*Chrysophtharta* sp. (Ch10) is closely related to *C. nobilitata* from which it may be distinguished by its different elytral pattern in life. The species most closely fits Blackburn's (1899) description of *C. debilis* (Chapuis) a locality of which was given by the original author (Chapuis 1877) as Tasmania.

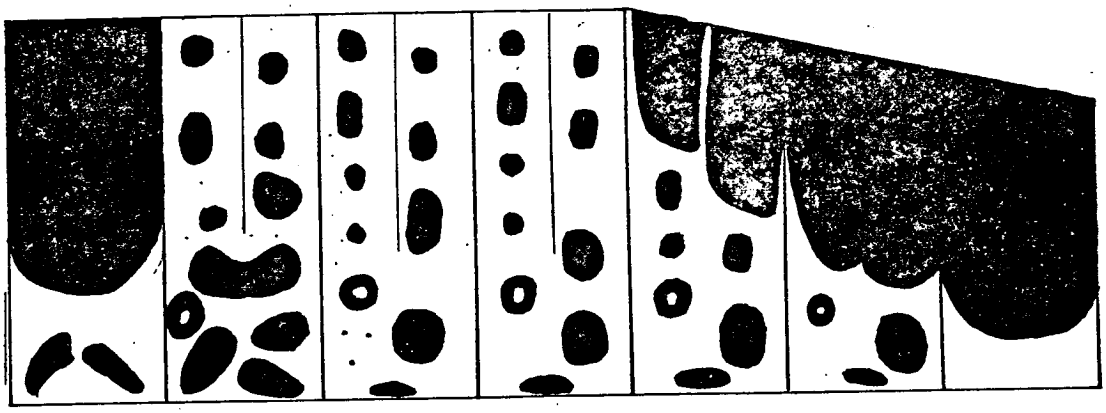
Larvae are solitary. The species is rare.

Figs. 68-70. Sclerite and tubercle diagrams of lateral view of thoracic and abdominal segments of second instar larvae of: (68) *Paropsis tasmanica*, (69) *P. aegrota*, (70) *P. porosa*. (Omitted segments identical to preceding segments.)

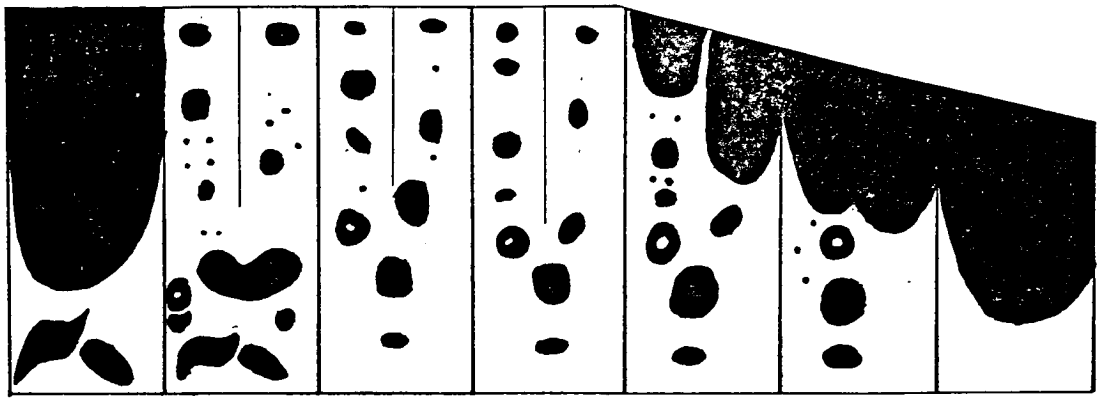
68



69

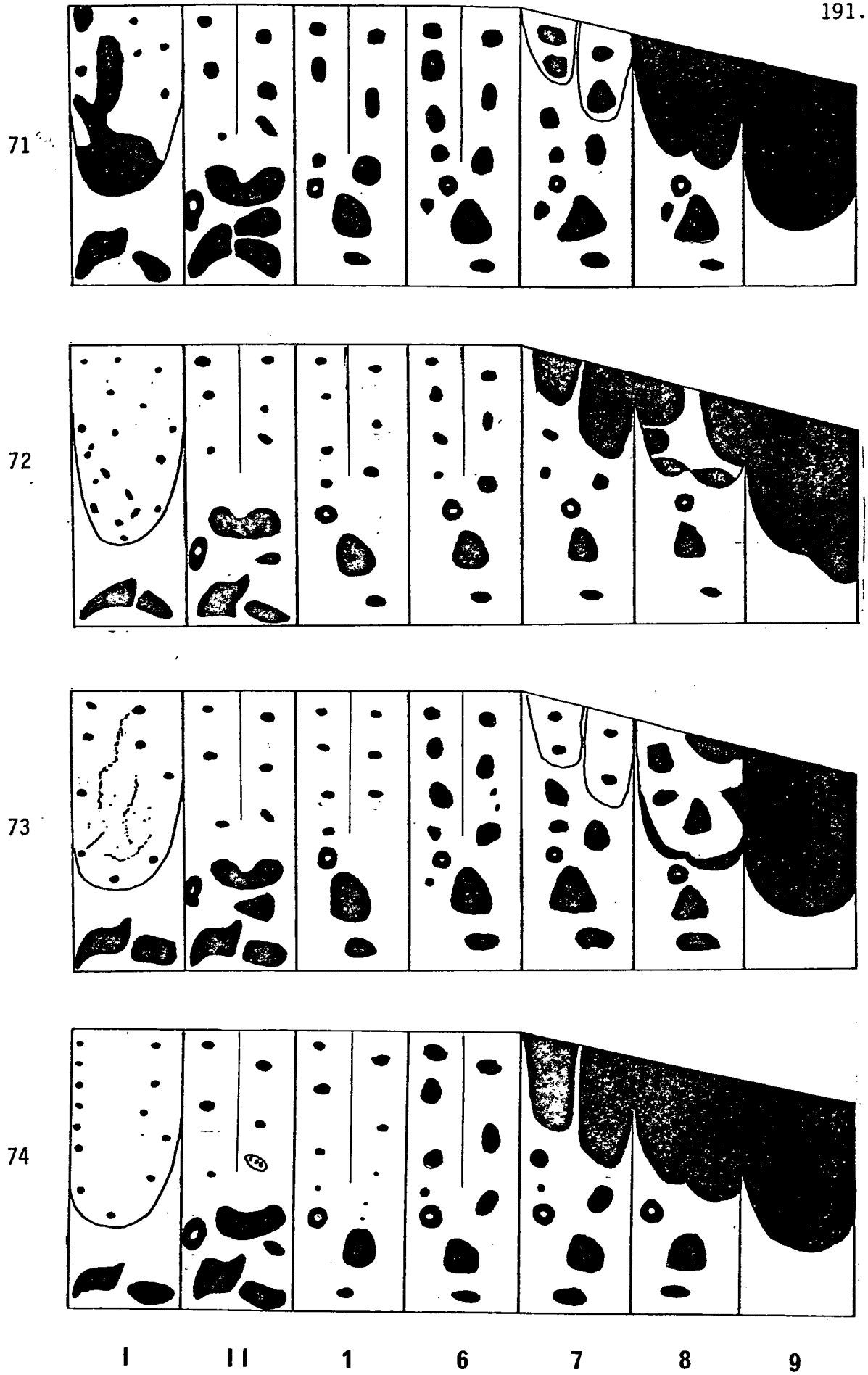


70



I II 1 6 7 8 9

Figs. 71-74. Sclerite and tubercle diagrams of lateral view of thoracic and abdominal segments of second instar larvae of: (71) *Paropsis dilatata*, (72) *P. charybdis*, (73) *Paropsis* sp. (Ps7), (74) *P. rubidipes*. (Omitted segments identical to preceding segments.)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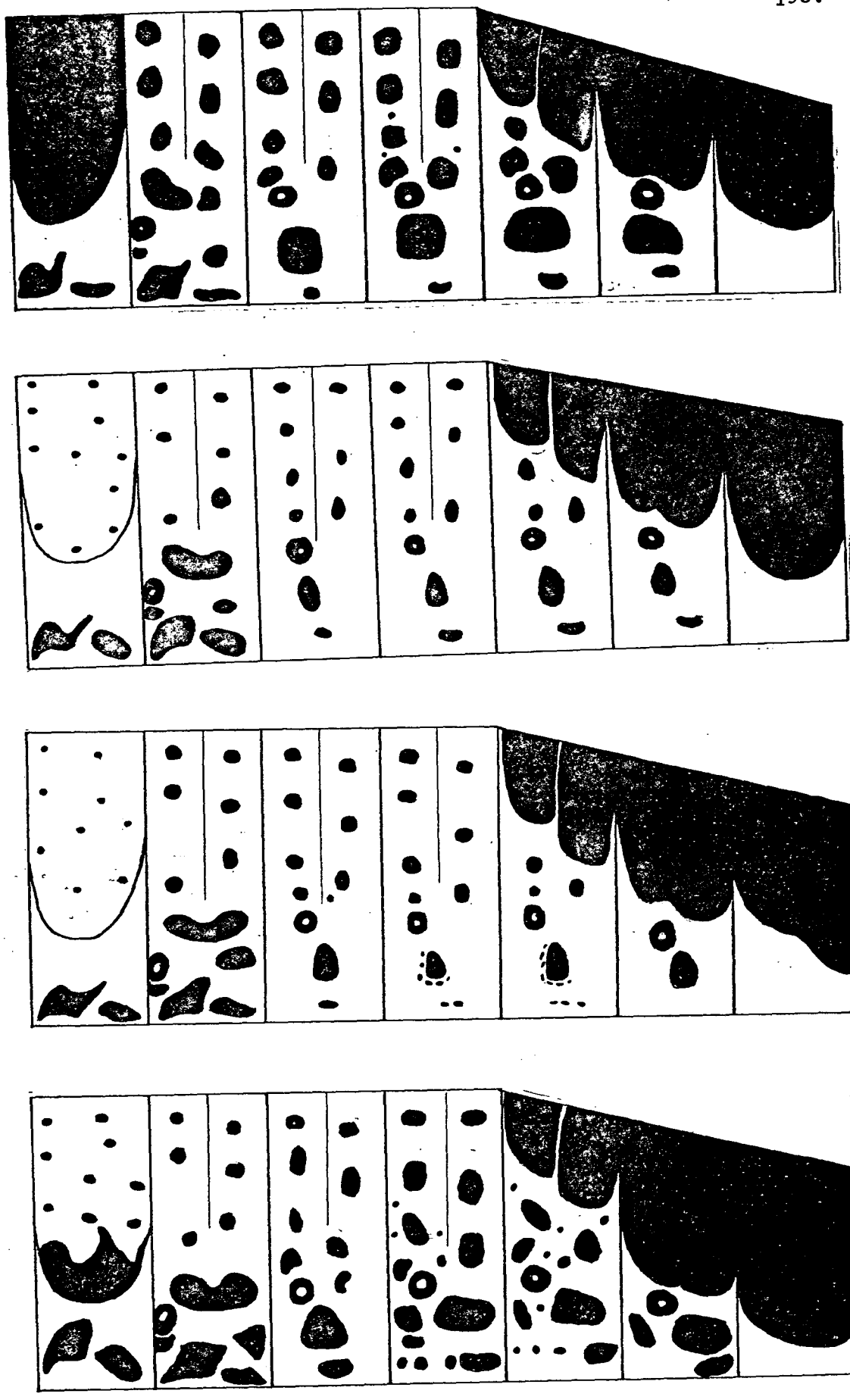
Figs. 75-78. Sclerite and tubercle diagrams of lateral view of thoracic and abdominal segments of second instar larvae of: (75) *Chrysophtharta agricola*, (76) *C. bimaculata*, (77) *Chrysophtharta* sp. (Ch13), (78) *C. aurea*. (Omitted segments identical to preceding segments.)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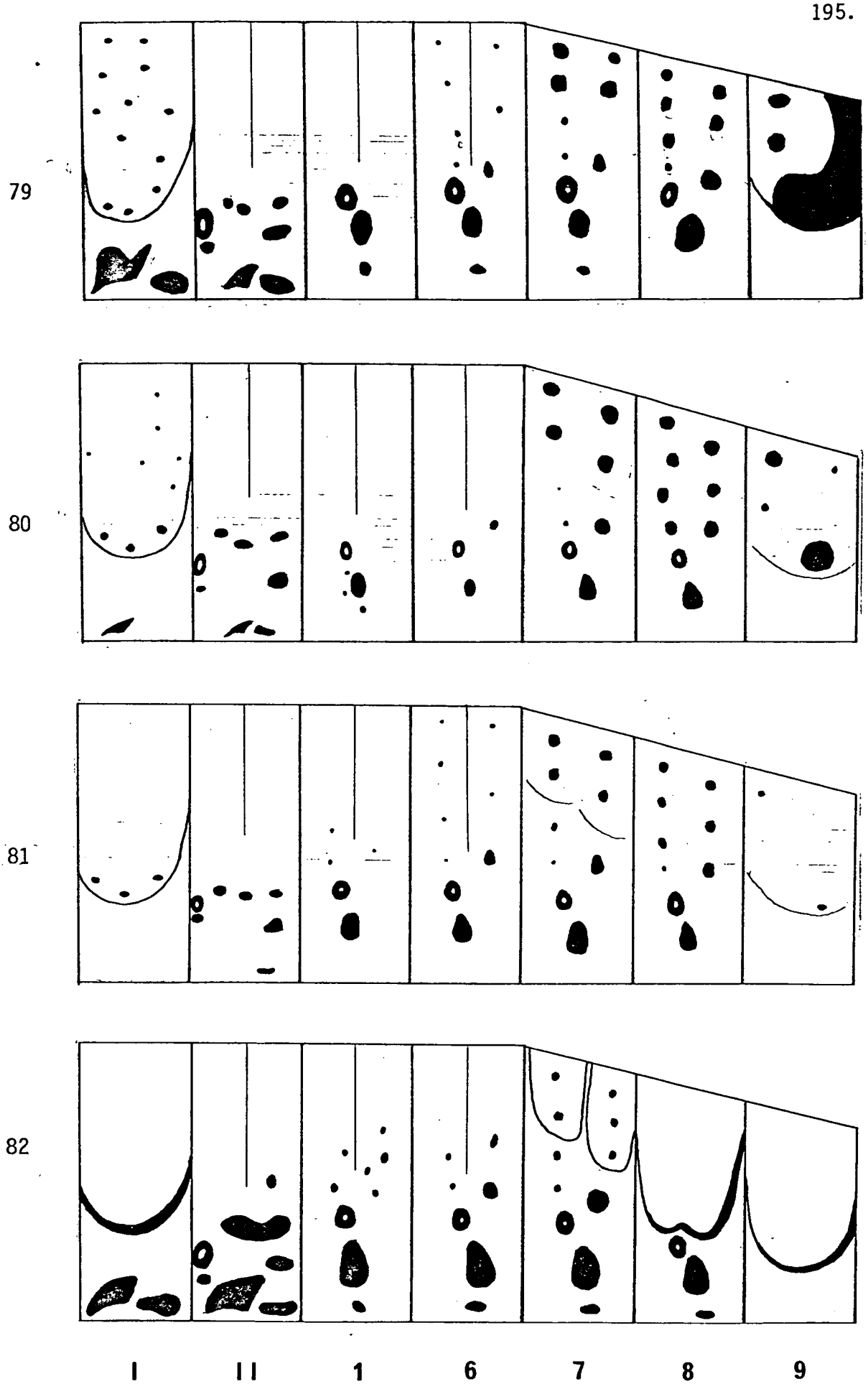
Figs. 79-82. Sclerite and tubercle diagrams of lateral view of thoracic and abdominal segments of second instar larvae of: (79) *Chrysophtharta decolorata*, (80) *Chrysophtharta* sp. (Ch11), (81) *Chrysophtharta* sp. (Ch12), (82) *C. simsoni*. (Omitted segments identical to preceding segments.)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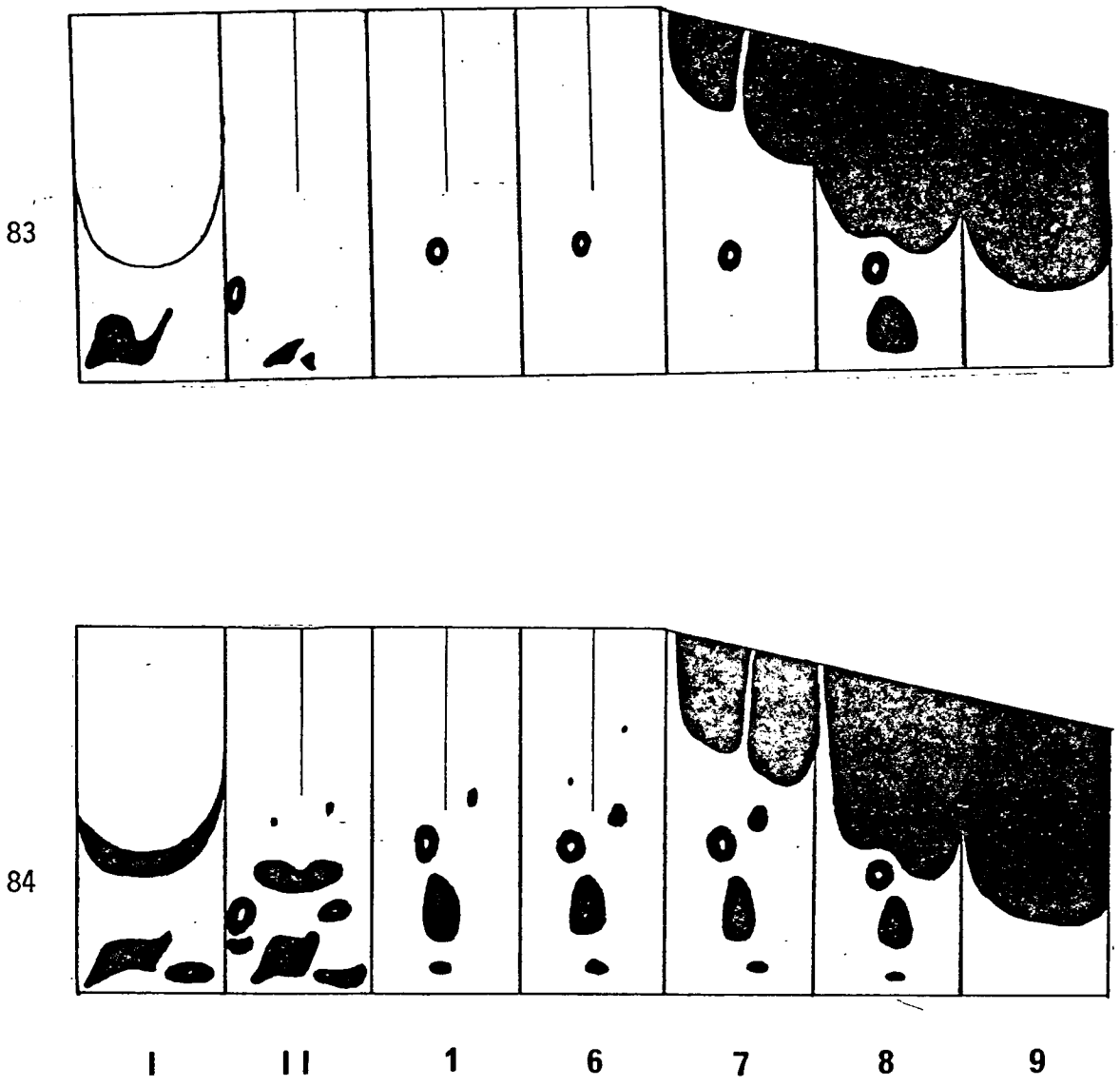



Figs. 83, 84. Sclerite and tubercle diagrams of lateral view of thoracic and abdominal segments of second instar larvae of: (83) *Chrysophtharta variicollis*, (84) *Chrysophtharta* sp. (Ch10). (Omitted segments identical to preceding segments.)

## 10. Genus *Paropsisterna* Motschulsky

*Paropsisterna* Motschulsky 1860, p. 193; Weise, 1901, p. 167; 1916, p. 159.

*Paropsis* Chapuis 1877, p. 73 (Group III); Blackburn, 1898, p. 221 (Group VI, Subgroup I).

### 10.1 Characters of Tasmanian species of *Paropsisterna*

Adults (Figs. 154-156) medium to large (8.5 to 13.5 mm long); highly glossy; elytral puncturation seriate in ten rows. Pronotum with well-defined sub-lateral fovae, entire margin. Elytral seriate puncturation fine to very fine, regular; interstitial puncturation very much finer than seriate puncturation.

Colour black or brown. Ventral surface black. Colour remaining stable in dry preservation.

Larvae (Figs. 188-190) tuberculate, densely setose in all instars; base body colour pale yellow-green to dark mauve-red.

Eggs (Figs. 217-219) with chorion thick, smooth or rugose.

## 10.2 Key to adults of Tasmanian species of *Paropsisterna*

1. Pale or dark brown species; pronotum pale brown with distinct black markings..... *nucea* (Erichson) (Pa1)

   Black species.....2

2. Large species (12 to 14 mm long); tarsae with white cilia..... *morio* (F.) (Pa3)

   Small species (8 to 10 mm long); base of head, proximal antennal segments, edge of pronotal and elytral margins brown..... *rufipes* (F.) (Pa2)

PAROPSISTERNA NUCEA (Erichson) (Pa1) (Figs. 30, 62, 107, 156, 188,217).

*Paropsis nucea* Erichson, 1842, p. 227; Blackburn, 1898, p. 226, 243.

*Paropsisterna nucea* Weise, 1916, p. 161.

Occurrence:-

MAKAA: Salmon R, 26.xi.1974, one adult.

MAKBE: "Surrey Hills", 6 km W St. Valentines Pk, 20.xii.1974, adults.

MATEG: Rocka Rvt, 1.xii.1974, four adults.

MATEH: Barton, 1.xii.1974, one adult.

MATEJ: Mt. Tor, 23.xi.1974, one adult.

SPEAB: Tiger Ck, 1.xii.1974, nine adults; The Lea, 4.i.1977, five adults; Tolman's Hill, 7.i.1977, three adults; Sandfly, 7.i.1977, five adults; York Town, 13.i.1977, one adult, 11 larvae; Frankford, 13.i.1977, one adult; Birralee, 13.i.1977, six adults, eight larvae; Salmon R, 17.i.1977, three adults; Black Charlies Opening, 27.i.1977, 12 adults; Rocka Rvt, 28.i.1977, 13 adults; Elephant Pass, 28.i.1977, one larva; Patersonia, 31.i.1977, nine adults, larvae.

SPEAH: Tooms Lake, 1.xii.1974, three adults.

SPIJA: Mt. Tor, 23.xi.1974, one adult.

SPIKK: Mt. Barrow, 10.xii.1972, adults; Mt. Tor, 16.i.1977, two adults; Railton, 18.i.1977, eight adults; Spring Beach, 28.i.1977, one adult; Gladstone, 28.i.1977, five adults; Pipers Brook, 28.i.1977, six adults; Lake Leake, 2.ii.1977, three adults.

SPINC: Bradys Lake, 19.i.1977, five adults.

SPINF: Poatina, 18.i.1877, one larva.

Female

Size 10.27±0.11 x 9.10±0.10 mm (N = 15).

Head finely but rugosely punctured. Pronotal disc smooth,

finely punctured; margins rugose, more coarsely punctured. Elytra with well-defined linear-seriate puncturation, interstitial puncturation very fine.

Colour of elytral disc shiny brown. Antennae black with exception of basal segments; head capsule black at base to at least one-third of distance of eyes from their posterior extremities; pronotum creamy-yellow with variable black markings; scutellum black; elytral margins creamy-yellow. Ventral surface and legs black.

Male

Size 9.10±0.10 x 6.67±0.06 mm (N = 15).

Larva

Head capsule widths: L1: 0.8 mm; L2: 1.2 mm; L3: 1.6 mm; L4: 2.3 mm.

Maximum length of approximately 14 mm.

Yellowish-green. Black body tubercle pattern present and complete; head black, protergite and abdominal segments VII-IX tuberculate in all instars. Densely setose, setae arising from tubercles.

Egg

Size 2.1 x 0.8 mm.

Pale yellow with thick, smooth, shining chorion. Cemented longitudinally in two rafts, "herring-bone" fashion on leaf surface.

Remarks

First described from Tasmanian material by Erichson (1842), the present identification is based on Blackburn's (1898) key and description. Adults superficially somewhat resemble adults

of *Chrysophtharta agricola* but they may be distinguished by the distinct prothoracic fovae, the elytral margins characteristic of *Paropsisterna* spp., and the regular, linear elytral seriate puncturation.

Larvae are solitary. The species is common and widespread throughout the island, but rarely encountered in large numbers in any locality. It is most commonly collected from Symphyomyrtus eucalypts. Egg batches and larvae are seldom encountered on the foliage of young saplings, indicating that the species may favour the crowns of mature trees.

PAROPSISTERNA MORIO (F.) (Pa3) (Figs. 64, 109, 154, 190, 219).

*Chrysomela morio* Fabricius, 1787, p. 66.

*Paropsis morio* Blackburn, 1898, p. 223, 227.

*Paropsisterna morio* Weise, 1916, p. 161.

Occurrence:-

SPIKK: Taroona, 20.ix.1973, adults (under bark); Ridgeway, 17.viii.1974, adults (under bark); Tolman's Hill, 24.xii.1976, one adult; Ridgley, 15.vii.1977, adults (under bark).

Female

Size 13.53±0.22 x 9.43±0.15 mm (N = 12).

Head finely, densely and evenly punctured with small unpunctured patches at base of antennae and midway between eyes and posterior epicranial arm. Pronotal disc finely punctured, margins slightly less finely punctured. Elytral seriate puncturation very fine; interstitial puncturation equally fine adjacent to seriate puncturation; finer in centres of interstices.

Colour uniformly shiny black. Tarsal ciliae white.

Male

Size 12.59±0.13 x 9.02±0.09 mm (N = 15).

Larva

Head capsule widths: L1: 0.9 mm; L2: 1.4 mm; L3: 2.2 mm; L4: 3.0 mm.

Maximum length of approximately 20 mm.

L1, 2 with thoracic segments pale green, abdominal segments mauve-red.

L3 with protergite, abdominal segments VII-IX tuberculate.

L4 with abdominal segments dark mauve.

Egg

Size 2.4 x 0.9 mm.

Dark "ash"-grey. Chorion smooth, tough, shining. Deposited longitudinally on leaf surface in a mass consisting of several irregular rows; up to 50 eggs per batch.

Remarks

This species, identified from Blackburn's (1898) key and description, was described by Fabricius (1787) from material collected in Tasmania by the Cook expedition of 1777. It is thus the first described paropsid species. *P. morio* is easily distinguished in the adult form by its large size and totally black colour (with the exception of the white tarsal cilia).

Larvae and adults feed mostly in the crowns of mature trees, but adults may be encountered in large numbers over-wintering under loose bark at the base of trunks of host trees, particularly of the Symphyomyrtus species *E. viminalis*.

PAROPSISTERNA RUFIPES (F.) (Pa2) (Figs. 31, 63, 108, 155, 187, 218).

*Chrysomela rufipes* Fabricius, 1801, p. 430.

*Paropsis rufipes* Olivier, 1807, p. 601.

*Paropsisterna rufipes* Weise, 1901, p. 168; 1916, p. 162.

*Paropsis circumdata* Newman, 1842, p. 415; Blackburn, 1898, p. 226, 245.

Occurrence:-

MAKAA: Pipers Brook, 28.i.1977, one adult.

MAKBE: "Surrey Hills", 7 km SW St. Valentines Pk, 30.x.1974, one adult; 30.xii.1975, four adults; Ridgley, 20.x.1977, one adult.

MATEG: Sandy Bay, 2.x.1974, one adult.

SPEAB: Sandfly, 7.i.1977, one adult; Birralee, 13.i.1977, one larva; Upper Esk, 31.i.1977, one adult.

SPIKK: Grove, 7.i.1977, one larva; Mt. Tor, 16.i.1977, three larvae; Preservation Bay, 17.i.1977, one adult; Ansons Bay, 28.i.1977, one adult.

Female

Size 9.41±0.14 x 6.58±0.08 mm (N = 7).

Head densely, finely but unevenly punctured. Pronotal disc very finely but unevenly punctured; margins more coarsely punctured. Elytra with seriate puncturation, fine, linear, spaces between punctures variable; interstitial puncturation extremely fine.

Colour shiny black with basal antennal segments, base of head, edges of pronotal and elytral margins and tarsae brown.

Male

Size 8.7 x 6.6 mm (N = 4).

Larva

Head capsule widths: L1: 0.9 mm; L2: 1.2 mm; L3: 1.6 mm; L4: 2.3 mm.

Maximum length of approximately 15 mm.

Pale greenish-yellow. Black body tubercle pattern present and complete; head, protergite and abdominal segments VII-IX tuberculate in all instars. Densely setose, setae arising from tubercles.

Egg

Size 2.6 x 1.1 mm.

Greyish-yellow with thick, rugose chorion. Cemented longitudinally in a raft consisting of two rather irregular rows. Approximate number per batch, 5-15.

Remarks

Blackburn (1898) refers to this species as *Paropsis circumdata* Newman. *P. circumdata* was synonymized with *Paropsisterna rufipes* (F.) by Weise(1901). The present identification is based on Blackburn's (1898) key. Adults somewhat resemble the melanic form of *Chrysophtharta agricola* but may be distinguished from them by the distinct prothoracic fovae, elytral margins characteristic of *Paropsisterna* spp., and brown base of head and edges of pronotum and elytra.

Larvae are solitary. The species is collected relatively infrequently.

## 11. Genus *Sterromela* Weise

*Sterromela* Weise, 1915, p. 436, 1916, p. 153.

*Paropsis* Chapuis, 1877, p. 73 (Group III); Blackburn, 1898, p. 221 (Group VI, Sub-group I), p. 656 (Group VI, Sub-group IV).

### 11.1 Characters of Tasmanian species of *Sterromela*

Adults (Figs. 157-160) large (11 to 17 mm long); convex or strongly laterally flattened; elytral puncturation seriate in ten rows. Pronotal margin entire. Elytral seriate puncturation coarse to moderately fine; deeply impressed giving elytra strongly striate appearance; interstitial puncturation very much finer than seriate puncturation.

Colour pale or dark brown. Colours remaining stable in dry preservation.

Larvae (Figs. 191-193) elongate, slender, highly mobile, with long legs; tuberculate, at least in early instars; non-setose. Base body colour of thoracic segments pale-yellow green; abdominal segments pink to dark mauve-red.

Eggs (Figs. 220-222) with chorion thick, smooth or rugose.

## 11.2 Key to adults of Tasmanian species of *Sterromela*

1. Species much flattened in lateral outline ..... 2

   Species normally convex in lateral outline .....3

2. Dark-brown species with prominent yellow vittae on elytra ..... *lineata* (Marsham) comb. n. (Sa4)

   Red-brown species with pale yellowish-brown elytral and pronotal margins ..... *subcostata*(Chapuis) (Sa1)

3. Pronotum with three round black maculae .... ..... *trimaculata* (Chapuis) (Sa2)

   Pronotum without black maculae ..... *Sterromela* sp. (Sa3)

STERROMELA LINEATA (Marsham) comb. n. (Sa4) (Figs. 65, 110, 158, 193, 222).

*Notoclea lineata* Marsham, 1808, p. 293.

*Paropsis lineata* Erichson, 1842, p. 118; Blackburn, 1898, p. 657, 663.

*Paropsisterna lineata* Weise, 1916, p. 161.

Occurrence:-

MAKAA: Highclere, 23.vii.1974, adults (under bark); Waterfall Bay, 20.v.1974, adults (under bark).

MATEG: Sandy Bay, 1.xi.1973, three adults (under bark), larvae.

Female

Size 10.89±0.16 x 7.12±0.10 mm (N = 14).

Very much flattened in lateral outline. Head and pronotal disc finely and evenly punctured. Margins of pronotum sparsely punctured. Prothoracic fovae absent. Elytral seriate puncturation linear, regular, deeply impressed; interstitial puncturation very fine.

Colour dark brown. On each elytron creamy-yellow markings consisting of two basal blotches between first and second and sixth and seventh elytral series respectively; a sub-marginal vitta running from base to apex between ninth and tenth series; a vitta from mid-point of each elytron to apex between third and fourth series; sometimes a faint vitta between fifth and sixth series towards apex.

Male

Size 10.45±0.21 x 6.70±0.12 mm (N = 9).

Larva

Head capsule widths: L1: 1.0 mm; L2: 1.4 mm; L3: 2.1 mm; L4: 2.8 mm.

Maximum length approximately 15mm.

Larva slender, highly mobile, legs elongate. Abdominal segments mauve-red, thoracic segments pale green. Head capsule, protergite, legs and abdominal segments VII-IX with black sclerotic areas; body tubercles black, complete.

Egg

Size 2.8 x 1.0 mm.

Pinkish-orange. Chorion rugose. Deposited in a mass under loose bark on trunk near base of tree.

Remarks

This species, adults of which are recognisable by their distinctive colouring and laterally flattened form, was identified from Blackburn's (1898) key and description. Weise (1916) included *S. lineata* in the genus *Paropsisterna*. The species has obvious close affinities to species of *Sterromela*, both in the larval and adult stages. The epipleuron is ciliate. The species is therefore here placed in the genus *Sterromela*.

Adults and larvae are usually collected under bark at the base of mature trees, suggesting that they feed in the crowns of these trees.

STERROMELA SUBCOSTATA (Chapuis) (Sa1) (Figs. 67, 112, 157, 191, 220).

*Paropsis subcostata* Chapuis, 1877, p. 75; Blackburn, 1898, p. 657, 663.

*Sterromela subcostata* Weise, 1915, p. 436; 1916, p. 153.

Occurrence:-

MAKAA: Tewkesbury, 15.viii.1974, 2 adults.

MAKCA: Florentine Valley, 2.iii.1976, adults; 15.vii.1975, one larva; Ridgley, 11.iv.1977, one adult.

Female

Size 12.90±0.11 x 8.58±0.07 mm (N = 8).

Elongate and flattened in lateral outline. Head evenly punctured with unpunctured patch behind posterior arm of epicranial suture. Pronotal disc unevenly punctured; margins more rugosely punctured. Prothoracic fovae shallow. Elytra with large, well-defined, deeply impressed,slightly irregular sinuous seriate puncturation; interstitial puncturation extremely fine. Epipleuron densely ciliate.

Colour red-brown with distinct yellow pronotal and elytral margins. Elytral series dark; interstices paler.

Male

Size 11.4 x 7.8 mm (N = 3).

Colour darker than female.

Larva

Head capsule width of L4 approximately 3.0 mm.

L4 with green thoracic segments, pink abdominal segments. Head capsule black. Protergite black laterally and anteriorly, minutely tuberculate in centre. Primary tubercles present laterally, dorsally irregularly tuberculate with secondary tubercles becoming faint towards centre.

Eggs

Size 3.0 x 1.4 mm.

Mauve-brown. Chorion smooth, shining. Deposited in an irregular mass under bark.

Remarks

Closely resembling the preceding species (*S. lineata*), in the laterally flattened form of the adult, this species was identified by Blackburn's (1898) key and description.

*S. subcostata* is a rare species and resembles *S. lineata* in habit.

STERROMELA TRIMACULATA (Chapuis) (Sa2) (Figs. 8, 32, 159).

*Paropsis trimaculata* Chapuis, 1877, p. 76; Blackburn, 1898, p. 226, 243.

*Sterromela trimaculata* Weise, 1915, p. 436; 1916, p. 153.

Occurrence:-

Campania, 5.vi.1973 (B. Saleh); Old Beach, 8.iii.1972 (J. Murton); Dynnyrne, 26.iii.1971 (J.R. Maynard); Mt. Nelson, 11.xii.1974 (K. Felton).

Female

Size 16.9 x 11.2 mm (N = 3).

Head finely and evenly punctured with unpunctured patch behind posterior arm of epicranial suture. Pronotal disc finely but unevenly punctured; margins rugosely punctured. Prothoracic fovae shallow. Elytra with well-defined, deeply impressed slightly irregular and sinuous seriate puncturation. Interstitial puncturation extremely fine.

Colour of dorsal surface pale yellow-brown. Head black at base and along posterior arm of epicranial suture (Fig. 33). Pronotum with three round black marks, one placed centrally, and one near each lateral margin; small faint oblique vitta posterior to each lateral blotch. Elytral series black; black blotch at humeral callous; elytral margins creamy-yellow.

Male, larvae, eggs unknown.

Remarks

Identified by Blackburn's (1898) key and description, this species is clearly recognizable by the three black marks on the pronotum.

*S. trimaculata* is a rare species, and was not encountered live in the present study.

STERROMELA sp. (Sa3) (Figs. 33, 66, 111, 160, 192, 221).

Occurrence:-

SPIKK: Burnie, 7.iv.1976, four adults.

Female

Size 16.0 x 10.7 mm (N = 3).

Similar to *S. trimaculata*. Head black at base with black colour drawn forward in "V" shape in centre. Pronotum unmarked. Elytral series black at base; seventh and eighth series only faintly black.

Male

Size 14.3 x 9.8 mm (N = 4).

Larva

Head capsule widths: L1: 1.2 mm; L2: 1.8 mm; L3: 2.6 mm; L4: 3.3 mm.

L1 with thoracic segments pale green; abdominal segments mauve-red. Head capsule, protergite, legs and abdominal tergites VII-IX black. Body tubercles present, black, pattern complete. Minutely setose.

L2, 3, 4 with dorsal loss of primary tubercles and development of irregular secondary tubercles; primary tubercles retained laterally.

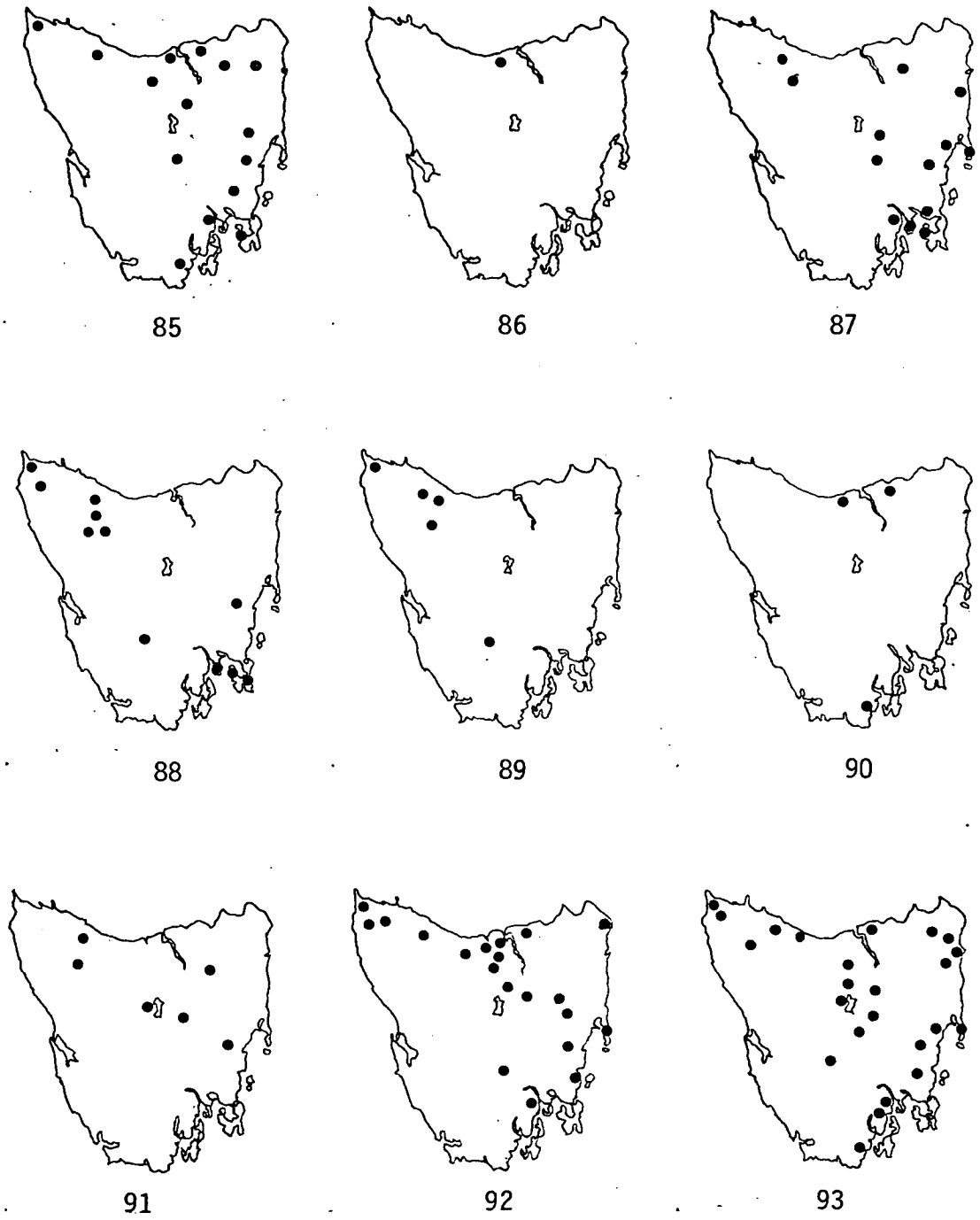
Egg

Size 3.0 x 1.4 mm.

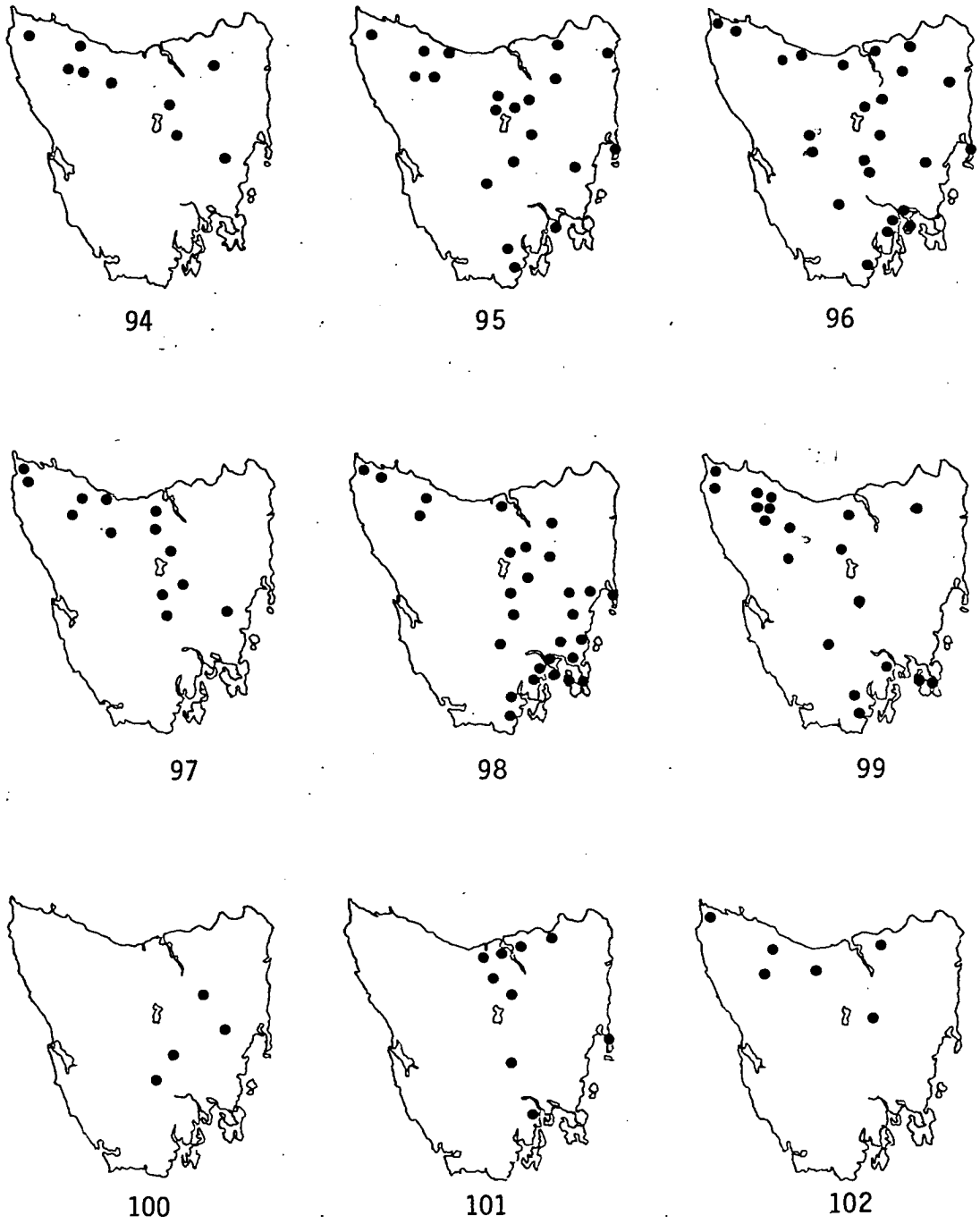
Mauve-brown. Chorion weakly rugose, shining. Deposited in an irregular mass under bark.

Remarks

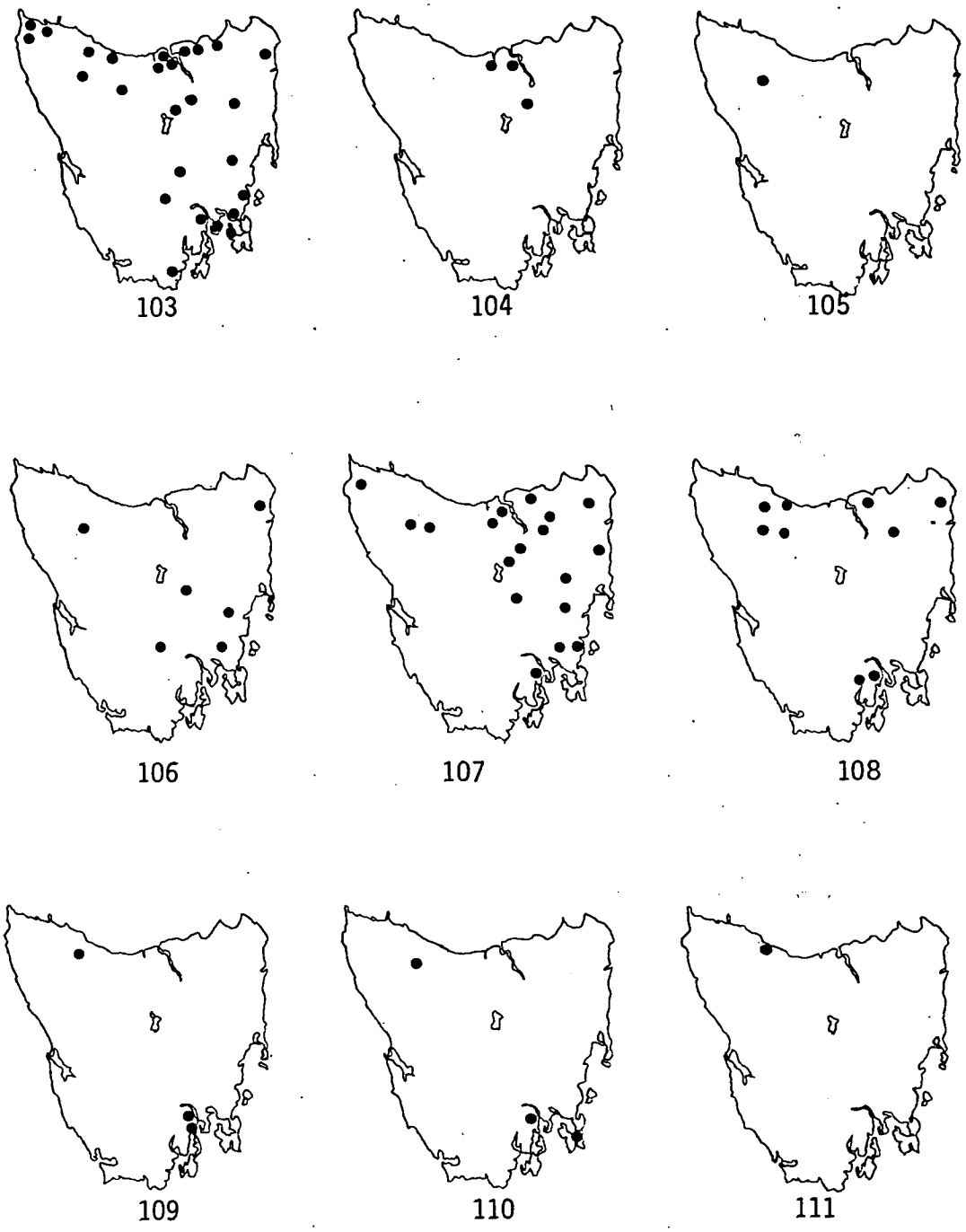
This "species" is probably a polymorphic form of *S. trimaculata*. Larvae resemble larvae of *S. lineata* and *S. subcostata* and are normally encountered under bark.



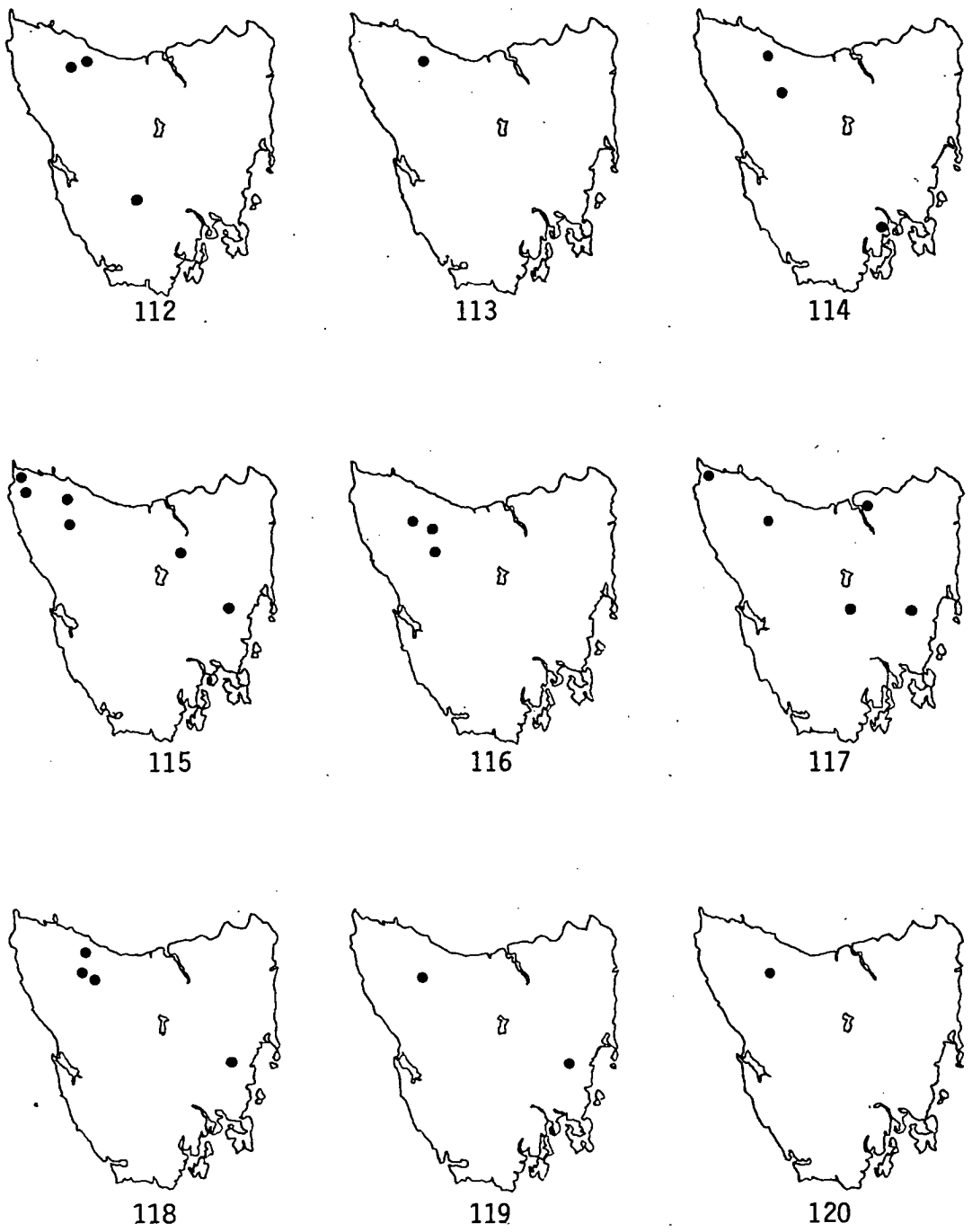

Figs. 85-93. Distributions of (85) *Paropsis tasmanica*, (86) *Paropsis* sp. (Ps9), (87) *P. charybdis*, (88) *P. dilatata*, (89) *Paropsis* sp. (Ps7), (90) *P. incarnata*, (91) *P. rubidipes*, (92) *P. porosa*, (93) *P. aegrota*.




Figs. 94-102. Distributions of (94) *Chrysophtharta lignea*, (95) *C. aurea*, (96) *C. decolorata*, (97) *C. agricola*, (98) *C. variicollis*, (99) *C. bimaculata*, (100) *Chrysophtharta* sp. (Ch12), (101) *Chrysophtharta* sp. (Ch13), (102) *Chrysophtharta* sp. (Ch8).




Figs. 103-111. Distributions of (103) *Chrysophtharta nobilitata*, (104) *Chrysophtharta* sp. (Ch11), (105) *C. simsoni*, (106) *Chrysophtharta* sp. (Ch10), (107) *Paropsisterna nucea*, (108) *P. rufipes*, (109) *P. morio*, (110) *Sterromela lineata*, (111) *Sterromela* sp. (Sa3).




Figs. 112-120. Distributions of (112) *Sterromela subcostata*, (113) *Trachymela* sp. (Ta7), (114) *Trachymela* sp. (Ta2), (115) *T. rugosa*, (116) *Trachymela* sp. (Ta4), (117) *T. papulosa*, (118) *Trachymela* sp. (Ta8), (119) *Trachymela* sp. (Ta6), (120) *Trachymela* sp. (Ta3).

# SECTION IV - ECOLOGICAL RELATIONSHIPS OF TASMANIAN *EUCALYPTUS*-DEFOLIATING PAROPSIDS WITH SPECIAL REFERENCE TO HOST-PLANT RELATIONSHIPS OF *CHRYSOPHTHARTA BIMACULATA* AND *C. AGRICOLA*.

## 1. Introduction

This section investigates some of the ecological relationships of the more frequently encountered paropsid species. Initial observations revealed the sympatric co-existence of many species on one to several species of host eucalypts. The within habitat abundances, phenologies and host preferences of different paropsid species suggested the employment of a variety of ecological strategies which permit this apparent co-existence.

Aspects of behaviour, phenology and host preference were studied in the field. The host preference of two abundant sympatric species, *Chrysophtharta bimaculata* and *C. agricola*, which were commonly encountered on different host species, were studied in detail in an insectary oviposition trial, and in laboratory feeding trials. In the feeding trials, the parameters of survival, rate of development, and final mass achieved were used to assess the favourability of host foliage for each species. Rates of consumption and gross conversion ratios were also calculated, and the two species compared with respect to rate of development, rate of food consumption, and efficiency of conversion of food.

Further feeding trials investigated more fully the host plant relationships of *C. agricola* and *C. bimaculata* in an attempt to evaluate reasons for the widespread pest status of the latter species in Tasmania.

## 2. Materials and Methods

### 2.1. Study Areas

The major part of this study was conducted in north western Tasmania, while the author was stationed at Ridgley ($41^{o}10'S$, $145^{o}50'W$), in forests south of Burnie owned by Associated Forest Holdings Pty. Ltd.,

Ecological and biological observations were made at many of the collecting localities listed in the Taxonomic Section (Section III).

Study sites in which intensive numerical studies were made were located at Ridgley and at "Surrey Hills". The Ridgley site consisted of a small arboretum plantation of *Eucalyptus gunnii* one to two metres high. The "Surrey Hills" sites consisted of:

1) a one or four metre high natural regeneration stand of *E. delegatensis* at Bunkers Road ("Bunkers Grass"), and

2) a one to three metre high mixed natural regeneration stand consisting of *E. delegatensis*, *E. nitida* and *E. dalrympleana* at Leven Road ("Leven"). (Fig. 222)

### 2.2. Sampling Methods

Quantitative general ecological sampling was conducted in the 1973/74 and 1974/75 seasons. Sampling in the first season was part of a general preliminary sampling programme conducted at a number of sites to monitor both pppulation levels and species diversity. Sampling at the "Leven" site in the 1974/75 season was undertaken specifically to investigate host-tree preference.

The shoot sample unit consisted of the terminal portion of a branchlet which constituted the current season's growth. Current

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Fig. 222: "Leven" study site, "Surrey Hills", photographed March 1974 showing regeneration of *E. delegatensis*, *E. dalrympleana* and *E. nitida* on which sampling was conducted.

season's foliage was distinguished from foliage of the previous season by its thinner texture and, sometimes, by its different colour. Leaves initiated in autumn expanded less, and were therefore smaller, than leaves initiated in spring. This was a further help in distinguishing previous season's from current season's growth. Shoot sample units normally consisted of the terminal 0.2 to 0.3 m of branchlets at the time of commencement of oviposition.

The method of tagging shoots used by Carne (1966a)was adopted at the Ridgley and Surrey Hills ("Bunkers Grass") sites in the 1973/74 season. A number of trees of close proximity and relative uniformity were selected and dominant shoot units were tagged at regular intervals around the circumference of each tree at heights convenient for close inspection. At Ridgley, five *E. gunnii* were selected, and five shoots tagged per tree, while at Bunkers Grass, ten trees were selected, and six shoots tagged per tree. Shoots were tagged with dark blue masking tape since it was considered that this was least likely to create artificial disturbance. Numbers of eggs and larvae of each paropsid species occurring on the tagged shoots were recorded at intervals of three to four days during periods of high activity, and at longer intervals when activity was lower.

At Leven, in the 1974/75 season, 500 shoots were chosen at random from each species of eucalypt on each date of sampling, and the presence of all stages of paropsids occurring on them was recorded. Shoots were sampled five times, at approximately two to three weekly intervals, from late December to early March.

2.3. Rearing Methods

A "constant environment" cabinet was constructed with a 40w "Lifeline Sylvania" one metre fluorescent tube at the top, and a thermostatically controlled "Simplex" HD5032 150 watt heating coil at the base (Fig. 223). The flucrescent tube was controlled by a time clock, which enabled variable photoperiod settings. The cabinet was provided with two steel mesh shelves which allowed for maximum light penetration and heat movement throughout the cabinet. Access was through sliding glass doors. The cabinet was placed in a room in which the temperature was buffered to a range of 20°C to 25°C. Relative humidity inside the cabinet ranged from 46 percent to 58 percent.

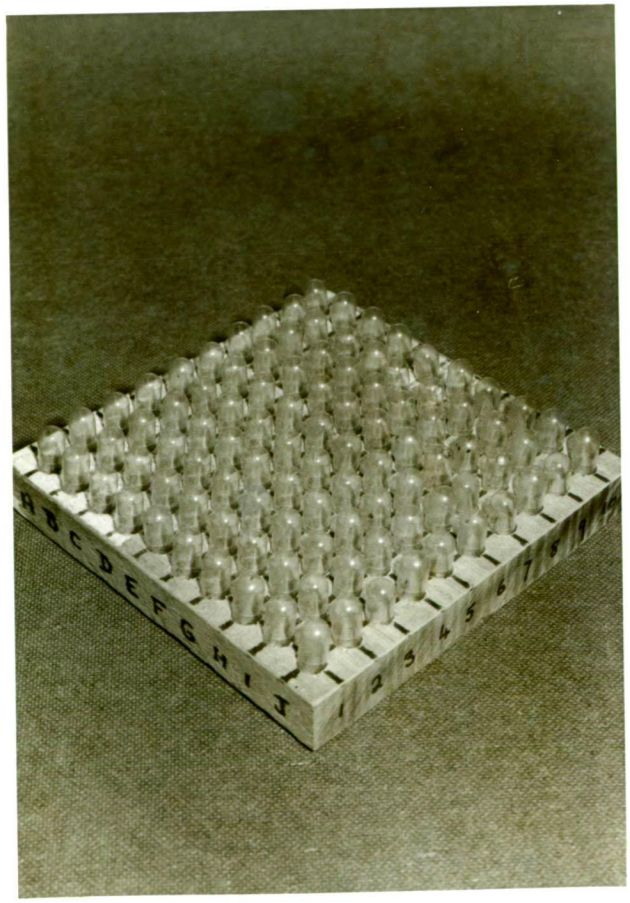
Live material was maintained in culture in plastic petri dishes as described in Section III (2.5), on fresh, palatable eucalypt leaves. Each petri dish was provided with a disc of filter paper to remove excess moisture. Petri dishes containing cultures were placed on moistened paper towelling in 20cm by 30cm by 4cm plastic meat trays with loosely fitting clear plastic lids (Fig. 223), and incubated in the "constant environment" cabinet. A maximum of twelve cultures were placed in each meat tray. Fresh foliage was supplied every one or two days, depending on stage of development and size of culture.

Two methods of rearing pupae were employed. The first method was described by Carne (1966a). Prepupae were placed in pupating cells made by sandwiching square pieces of cellular plastic link matting (cells 13mm square) between two sheets of glass. The matting was cut to provide 100 cells, and the top sheet of glass was marked with symbols aligned with each row and column of cells, thus providing co-ordinates by which the position of any one prepupa could be defined.

Fig. 223: Rearing method for paropsid adults and larvae in controlled environment cabinet showing petri dishes in meat trays on steel mesh shelf. Note wet and dry bulb thermometer for measuring relative humidity, and heating coil taped to floor of cabinet.

Fig. 224: Rearing method for pupae showing gelatin capsules individually identifiable by row and column co-ordinates marked on wooden base.

223

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The second method (Fig. 224) has also been used by P.B. Carne (*pers. comm.*). Prepupae were placed in gelatin capsules (Parke-Davis 000). Holes to support the capsules were drilled in blocks of wood (165 x 165 x 20 mm) in a 10 x 10 grid, and row and column co-ordinates marked on the blocks. The advantage of this system was that pupae were less susceptible to death through desiccation.

## 2.4. Laboratory Feeding Trials

Field collected egg batches of *C. bimaculata* and *C. agricola* were incubated in the constant environment cabinet. Larvae hatching over a 24 hour period were used to establish feeding trials.

Larvae in feeding trials were reared on foliage in petri dishes. Twenty-five newly emerged first instar larvae were placed on foliage in each petri dish using a fine hair paint brush, and each treatment was replicated four times. Cultures were incubated at constant temperature and at a 16 hour photophase. Fresh foliage was provided every one to two days, and old foliage removed. At the conclusion of feeding, numbers of larvae remaining in each culture were counted, and larvae were placed in pupating cells as described. In all feeding trials, the juvenile form of foliage of each of the eucalypt species tested was used.

### 2.4.1. Feeding Trial 1

In this trial, *C. bimaculata* and *C. agricola* larvae were reared on foliage of each of *E. delegatensis* and *E. dalrympleana* from the Leven study site. Four replicates of each of four treatments of *C. bimaculata* on *E. delegatensis*, *C. bimaculata* on *E. dalrympleana*, *C. agricola* on *E. delegatensis*, and *C. agricola* on *E. dalrympleana* were established with newly emerged, weighed

larvae and maintained at 20°C and 16 hours photophase. On each of two successive following days larvae which died through failure to establish feeding were replaced with other larvae which emerged over the same period.

Larvae were transferred to clean petri dishes containing fresh, weighed young foliage collected from adjacent to the field study area every one to two days, and the uneaten foliage remaining cleaned and weighed. Four control dishes of each of *E. delegatensis* and *E. dalrympleana* were maintained, and the foliage weighed and changed at the same time as that in the cultures. A correction factor for loss of mass due to transpiration over each period was applied to the masses of foliage remaining at the end of each period. These corrected masses were subtracted from the mass of foliage at the start of each period, the difference being the mass of fresh foliage consumed. Cumulative masses of foliage eaten per larva were obtained by dividing amounts eaten in each culture, for each period, by the number of larvae surviving in that culture, and summing amounts eaten for each period. Masses of fourth instar larvae were obtained as they completed feeding and became prepupae, and date of completion of feeding recorded.

Adults were weighed upon emergence from pupation and the date of each emergence was recorded.

### 2.4.2. Feeding Trial 2

The treatments consisted of *C. bimaculata* and *C. agricola* reared on foliage of each of *E. delegatensis, E. regnans, E. globulus* and *E. viminalis* collected from Ridgley. Cultures were incubated at 23°C, and date of pupation was recorded.

2.4.3. Feeding Trial 3

The treatments consisted of *C. bimaculata* reared on foliage of *E. obliqua, E. delegatensis, E. regnans, E. fastigata* and *E. nitida*. Foliage was collected from Ridgley. Cultures were incubated at 23°C, and date of pupation was recorded.

2.5. Insectory Oviposition Trial

Three ovipositing females, and three mature males of each of *C. bimaculata* and *C. agricola* were collected from their preferred hosts and introduced into a small nylon mesh cage (30 x 30 x 30 cm) which was placed outside in a sheltered position, mid-season, 1974/75. The wire floor of the cage was provided with leaf litter for shelter. Carefully matched, cut shoots of *E. delegatensis* and *E. dalrympleana* from the Leven study site were placed in water-filled conical flasks plugged with cotton wool, and a shoot of each species placed in opposite corners of the cage. Shoots were replaced every three to four days, and their placement in the cage alternated. Tallies of egg batches of each species placed on the shoots were maintained for 43 days.

## 3.3. Observations and Results

### 3.3.1. Bionomics of the More Commonly Encountered *Eucalyptus*-defoliating Paropsid Species

Most paropsid species encountered on eucalypts could be placed in one of two groups based on five main bionomical characteristics (Table 4). Species showing mainly group one characteristics occurred in the genera *Paropsis*, *Chrysophtharta* and *Paropsisterna*, while species showing mainly group two characteristics occurred in the genera *Trachymela* and *Sterromela*. *Trachymela rugosa* (Chapuis) was anomalous, and showed group one characteristics, although taxonomically belonging in the genus *Trachymela*. *Sterromela lineata* (Marsham) comb.n., which showed group two characteristics, was transferred from the genus *Paropsisterna* on sound taxonomic grounds (Section III).

Among group one species, *Chrysophtharta aurea* (Blackburn) and *C. lignea* (Erichson) showed anomalous oviposition behaviour. Eggs of *C. aurea* were not deposited on foliage in the field, and in fact, were never located, although this species oviposited copiously in the laboratory. *C. lignea* was ovoviviparous. The fully developed embryo was deposited on foliage enclosed in a fine membrane which ruptured shortly after oviposition.

A striking characteristic of larvae of some group one species was the possession of aposematic coloration. Such coloration normally consisted of strongly contrasting black, orange, yellow and white bands, spots or blotches. All species with aposematically coloured largae showed aggregative, gregarious larval behaviour (Table 5). Larval colonies in which larvae were aposematically coloured usually showed a distinct pattern of arrangement,

Table 4.

Bionomical characteristics identifying two groups of *Eucalyptus*-defoliating paropsids.

| | Group 1 | Group 2 |
|---|---|---|
| 1. | Eggs deposited on or near foliage on which larvae feed. | Eggs concealed under bark and often near base of trunk. |
| 2. | Larvae feed and rest on foliage during day; some species form gregarious larvae aggregations. | Larvae feed nocturnally and rest under bark during day. |
| 3. | Immature stages always occur in summer period. Adults overwinter. | Immature stages may occur at any time of the year. |
| 4. | Primitive body tubercle pattern, sclerotic areas and colourings usually modified, at least in later larval instars in which modified colourings and markings serve a cryptic or aposematic function. | Larvae retain primitive black body tubercle markings and sclerotic areas; thoracic colour pale green, abdominal colour dark reddish-brown. |
| 5. | Larvae short-legged, sluggish, and show strong defensive reaction. | Larvae long legged, highly mobile, and show weak defensive reaction. |
| Genera: | *Paropsis*<br>*Chrysophtharta*<br>*Paropsisterna*<br>*Trachymela rugosa* | Genera: *Trachymela*<br>*Sterromela* |

Table 5.

Classification of larval colours and markings and larval aggregation behaviour* of selected "group one" paropsid species.

| Species | Larval colours and markings | Larval aggregation behaviour |
|---|---|---|
| *Paropsis aegrota* | aposematic | + |
| *P. tasmanica* | aposematic | + |
| *P. charybdis* | indefinite | slight |
| *P. dilatata* | cryptic | slight |
| *P. rubidipes* | cryptic | - |
| *Chrysophtharta bimaculata* | indefinite | + |
| *C. agricola* | aposematic | + |
| *C. variicollis* | aposematic | + |
| *C. decolorata* | cryptic | - |
| *C. nobilitata* | cryptic | - |
| *C. aurea* | cryptic | - |
| *C. lignea* | cryptic | - |
| *Paropsisterna nucea* | indefinite | - |
| *Trachymela rugosa* | cryptic | slight |

*Larval aggregation behaviour:

+ : strong aggregation behaviour

slight : slight tendency to aggregate

- : no aggregation behaviour

(a)

(b)

Fig. 225: Aposematic markings and characteristic aggregation patterns of larvae of (a) *Paropsis aegrota* in alarm position, (b) *Chrysophtharta variicollis*.

characteristic of a species (Fig. 225). Not all species showing colonial larval behaviour had aposematically coloured larvae, e.g. the very common species *Chrysophtharta bimaculata* (Olivier).

Cryptically coloured larvae were various shades of pinkish, reddish, or yellowish, or brownish-green. Fourth instar larvae of *P. dilatata, P. rubidipes* and *T. rugosa* mimicked leaf galls which frequently occurred on eucalypt leaves. Larvae of group two species were all green to mauve-red and did not show aposematic or cryptic colour modification.

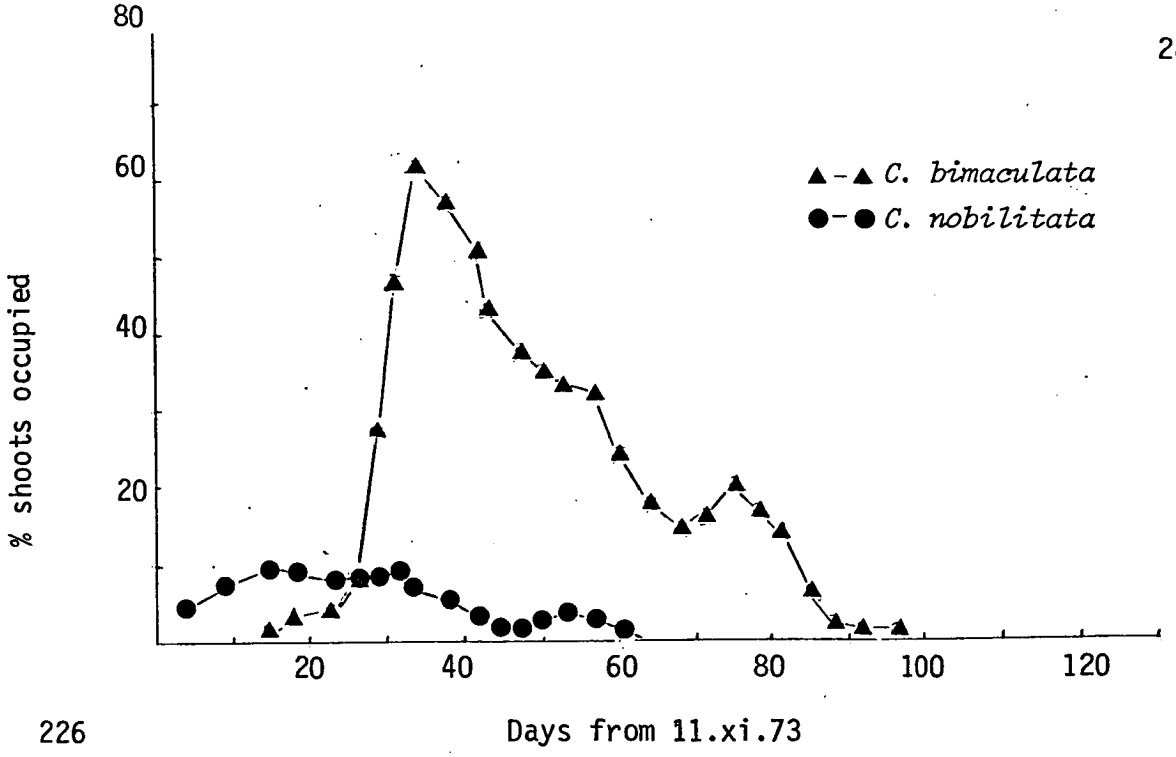
Adult beetles of the genera *Paropsis* and *Trachymela* mimicked leaf and stem galls, leaf lesions and, sometimes, fruits of eucalypts. The brilliant colours of some adult *Chrysophtharta* spp. possibly had an aposematic function.

### 3.3.2. Phenological Adaptations

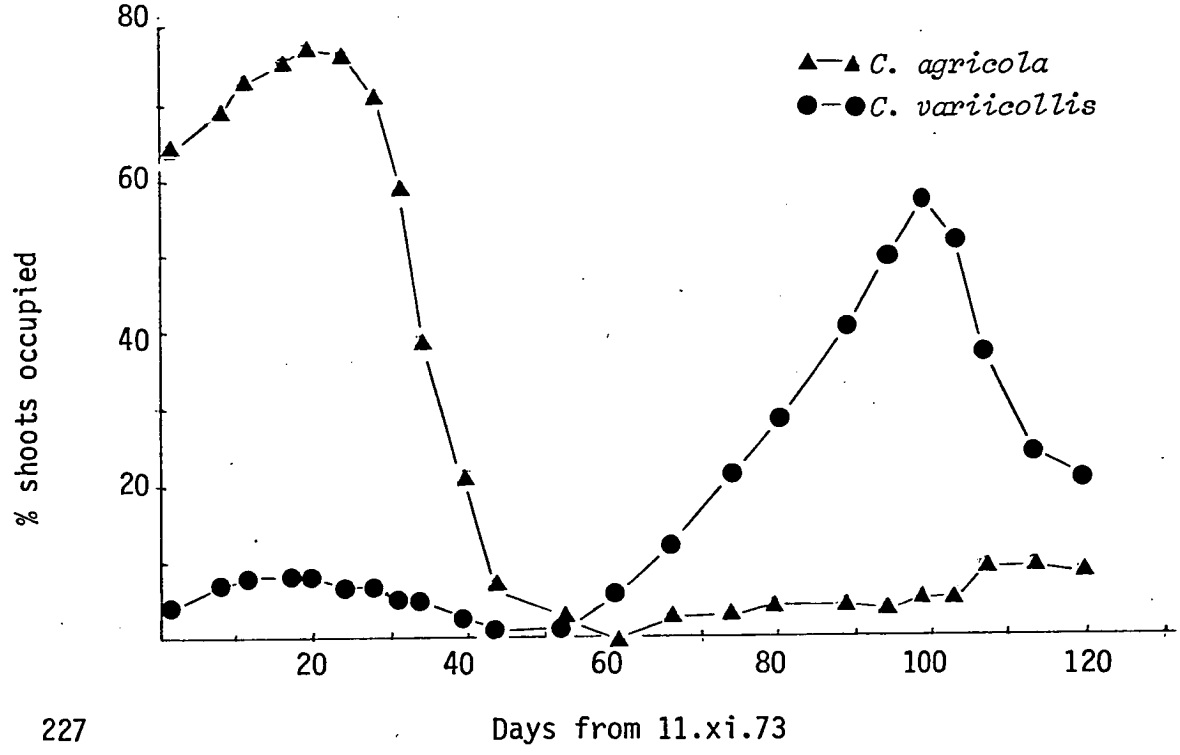
In the course of preliminary sampling during the 1973/74 season, two cases were observed where two different paropsid species feeding on the same host trees avoided direct competition by their different phenological adaptations.

At Ridgley, populations of closely related species *Chrysophtharta agricola* and *C. variicollis* were sampled on five young *E. gunnii* saplings (Fig. 226) (Appendix 1.1). Early in the season eggs and larvae of *C. agricola* predominated. After recovery of trees from defoliation, mainly due to *C. agricola,* a second oviposition, mainly by *C. variicollis*, occurred in January. *C. variicollis* predominated in the latter part of the season.

A similar instance of phenological separation of populations of *C. bimaculata* and *C. nobilitata* was observed on ten *E. delegatensis* saplings at Bunkers Grass, Surrey Hills (Fig. 227) (Appendix 1.2).




226




227

Figs. 226, 227. Percentage of shoots occupied by immature stages (eggs and larvae) at successive sampling dates (3-date running averages), throughout the 1973/74 season of: (226) *Chrysophtharta nobilitata* and *C. bimaculata* on *E. delegatensis* (60 fixed shoots) at Bunkers Grass "Surrey Hills", and (227) *C. agricola* and *C. variicollis* on *E. gunnii* (25 fixed shoots) at Ridgley.

Although *C. bimaculata* was the most abundant species at this site for most of the season, *C. nobilitata* eggs and larvae were encountered at the site early in the season, before *C. bimaculata* appeared. *C. nobilitata* oviposited on buds and very young partially expanded leaves, which were unsuitable as oviposition sites for *C. bimaculata*.

### 3.3.3. Field observed host specificity of *C. bimaculata*, *C. agricola*, *C. aurea*, *C. nobilitata*, *P. aegrota* and *T. rugosa*

The spatial and temporal distribution of adults, eggs and fourth instar larvae of the six most abundant species sampled at the Leven study site during the 1974/75 season is summarized in Table 6.

The two most abundant species were *C. bimaculata* and *C. agricola*, both adults and immatures of which occurred most frequently on *E. delegatensis* and *E. dalrympleana* respectively. *C. bimaculata* adults and eggs were also encountered on *E. nitida*, while adults only were encountered on *E. dalrympleana*. *C. agricola* adults, eggs and larvae were also encountered on *E. delegatensis*, but this species never occurred on *E. nitida*. Two of the three host eucalypt species were classified in the *Monocalyptus* subgenus (*E. delegatensis* and *E. nitida*) while *E. dalrympleana* was placed in the *Symphyomyrtus* subgenus. *E. delegatensis* was placed in the series Obliquae, while *E. nitida* occurred in the series Piperitae.

The other four paropsid species were sampled too infrequently to enable speculation on host preferences, based on the results shown. However, *E. nitida* appeared less favourable than either *E. delegatensis* or *E. dalrympleana*.

Table 6.

Spatial and temporal distribution of adults (A), eggs (E), and fourth instar larvae (L4), of the major paropsids occurring on MAKBE *E. delegatensis*, MATEJ *E. nitida* and SPINC *E. dalrympleana* expressed as % of shoots occupied, at Leven study site,1974-75 season.

| | | 27.xii.74. | | | 14.i.75. | | | 29.i.75. | | | 17.ii.75. | | | 6.iii.75. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Host | A | E | L4 | A | E | L4 | A | E | L4 | A | E | L4 | A | E | L4 |
| *Chrysophtharta bimaculata* | MAKBE | 1.5 | 10.8 | | 0.2 | 6.0 | | 0.8 | 6.6 | 0.4 | 0.4 | 4.6 | 2.2 | 0.4 | 1.4 | 2.2 |
| | MATEJ | 0.2 | 0.2 | | | | | 0.2 | | | 0.4 | 0.2 | | | | |
| | SPINC | 0.6 | | | | | | 0.6 | | | | | | 0.2 | | |
| *C. agricola* | MAKBE | 0.2 | 1.2 | | | | | | 0.4 | 0.2 | | | | | | |
| | MATEJ | | | | | | | | | | | | | | | |
| | SPINC | 2.4 | 11.4 | | 1.2 | 4.6 | 0.2 | | 5.2 | 1.0 | | 1.2 | 2.8 | | | 1.4 |
| *C. aurea** | MAKBE | | | | 0.2 | | | | | | | | | | | |
| | MATEJ | 2.6 | | | | | | 0.4 | | | 0.2 | | | | | 0.2 |
| | SPINC | | | | | | | | | | | | | | | |
| *C. nobilitata* | MAKBE | 0.4 | 5.4 | | 0.2 | 3.6 | 0.2 | | 1.2 | 0.2 | | | 0.2 | | | 0.2 |
| | MATEJ | 0.6 | 0.6 | | 0.2 | 1.0 | | | 1.0 | | 0.2 | | | | | 0.2 |
| | SPINC | 0.2 | 0.6 | | 0.2 | 0.8 | | | | | | | | | | |
| *Paropsis aegrota* | MAKBE | 0.2 | | | | | | | | | | | | | | |
| | MATEJ | 0.2 | | | | | | | | 0.2 | | 0.2 | | | | |
| | SPINC | | 0.4 | | | 0.6 | | | | | | | 0.6 | | | |
| *Trachymela rugosa* | MAKBE | 0.2 | 0.6 | | | 0.6 | | 0.2 | 0.2 | 0.2 | | 0.2 | | 0.2 | | |
| | MATEJ | | | | 0.2 | | | | | | | 0.2 | | | | |
| | SPINC | | | | | 0.2 | | 0.2 | | | | | | | | |

*Eggs of *C. aurea* are not placed on foliage.

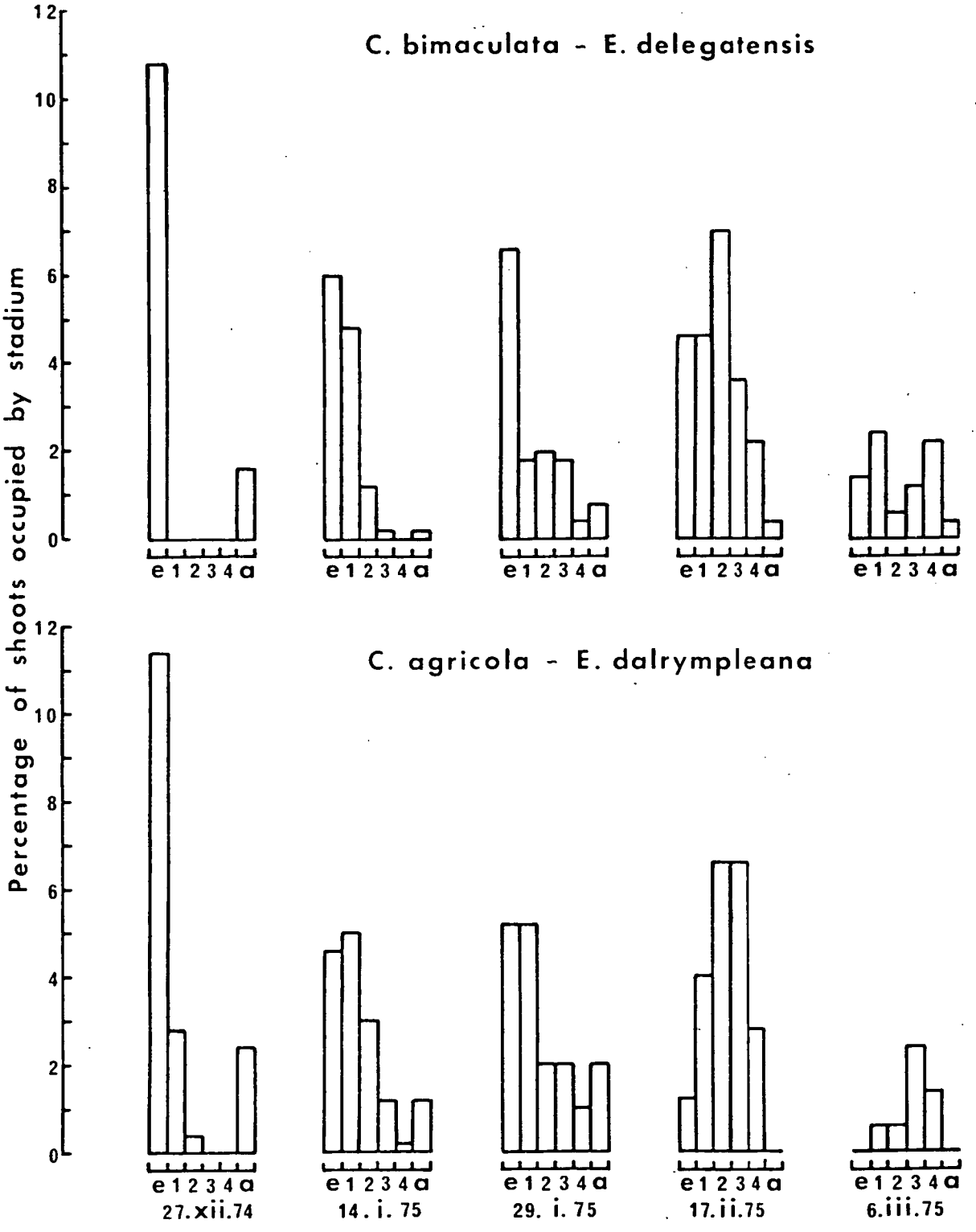



Fig. 228. Percentage of shoots (n = 500) occupied by successive stages of *C. bimaculata* and *C. agricola* on *E. delegatensis* and *E. dalrympleana* respectively at Leven study site ("Surrey Hills") on successive dates of sampling: e - eggs, 1, 2, 3, 4, - 1st, 2nd, 3rd, 4th instar larvae, a - adults.

The synchrony of the phenologies of *C. bimaculata* and *C. agricola* on their respective preferred hosts is shown in Fig. 228. Both hosts were favourable for oviposition and as larval food over a similar period of time.

3.3.4. Oviposition specificity of *C. bimaculata* and *C. agricola*

Total egg batches deposited by three mature, adult, field-collected females of *C. bimaculata* and of *C. agricola*, when presented with a choice of fresh *E. delegatensis* and *E. dalrympleana* shoots in an outside insectary over 43 days are shown in Table 7. Interaction $\chi^2$ shows the data to be heterogeneous ($P < .005$), indicating an oviposition preference of *C. bimaculata* for *E. delegatensis*, and of *C. agricola* for *E. dalrympleana*.

3.3.5. Survival, rate of growth, rate of food consumption and conversion ratios of *C. bimaculata* and *C. agricola* larvae reared on foliage of *E. delegatensis* and *E. dalrympleana* (Appendix 2)

There was a highly significant interaction between insect and host with respect to larval survival (Table 8). Survival of *C. bimaculata* larvae was significantly lower on foliage of *E. dalrympleana* than on *E. delegatensis* foliage. There was no significant difference between the survival of *C. agricola* on foliage of *E. delegatensis* and *E. dalrympleana*. On *E. delegatensis*, there was no significant difference between the survival of *C. bimaculata* and *C. agricola* larvae.

The total duration of the larval feeding stages of *C. bimaculata* on *E. delegatensis* was significantly shorter than on *E. dalrympleana* (Table 9). There was no significant difference between the duration

Table 7.

Numbers of egg batches deposited by three field-collected, sexually mature females of each of *C. bimaculata* and *C. agricola* on shoots of *E. delegatensis* and *E. dalrympleana* in an outside cage, 4.i.-16.ii.75.

| | *C. bimaculata* | *C. agricola* | Total |
|---|---|---|---|
| *E. delegatensis* | 31 | 7 | 38 |
| *E. dalrympleana* | 6 | 35 | 41 |
| Total | 37 | 42 | 79 |

Interaction $\chi^2$ = 32.86*** (0.1%)

Table 8.

Survival of larvae to prepupal stage of *C. bimaculata* and *C. agricola* fed *E. delegatensis* and *E. dalrympleana* foliage at 20°C, 16 hours photophase.

| Treatment | Mean Survival (± S.E.) | (%) |
|---|---|---|
| (a) *C. bimaculata* - *E. delegatensis* | 20.25 ± 1.25 | 81 |
| (b) *C. bimaculata* - *E. dalrympleana* | 12.50 ± 1.66 | 50 |
| (c) *C. agricola* - *E. delegatensis* | 16.75 ± 2.50 | 67 |
| (d) *C. agricola* - *E. dalrympleana* | 21.00 ± 1.00 | 84 |

Analysis of Variance

| Source of Variance | d.f. | Mean Square | F |
|---|---|---|---|
| Treatments | 3 | 60.42 | 5.24* |
| Insect (I) | 1 | 25.00 | 2.17 |
| Host (H) | 1 | 12.25 | 1.06 |
| I x H Interaction | 1 | 144.00 | 12.48*** |
| Residual | 12 | 11.54 | |

(* : 5%; *** : 0.5%)

L.S.D. Tests (12 d.f.)

lsd (.05) = 5.23 larvae; lsd (0.1) = 7.33 larvae

$\bar{x}_a - \bar{x}_b = 7.75^{***}$

$\bar{x}_d - \bar{x}_c = 4.25$ ns

$\bar{x}_a - \bar{x}_c = 3.50$ ns

(*** = 0.1%)

Table 9.

Duration (days) of larval feeding stage of *C. bimaculata* and *C. agricola* fed *E. delegatensis* and *E. dalrympleana* foliage at 20°C, 16 hours photophase.

| Treatment | Mean (± S.E.) |
|---|---|
| (a) *C. bimaculata* - *E. delegatensis* | 13.02 ± 0.13 |
| (b) *C. bimaculata* - *E. dalrympleana* | 17.41 ± 0.40 |
| (c) *C. agricola* - *E. delegatensis* | 16.05 ± 0.24 |
| (d) *C. agricola* - *E. dalrympleana* | 16.64 ± 0.34 |

Analysis of Variance

| Source of Variance | d.f. | Mean Square | F |
|---|---|---|---|
| Treatments | 3 | 14.82 | 42.18*** |
| Insect (I) | 1 | 5.12 | 14.57*** |
| Host (H) | 1 | 24.88 | 70.81*** |
| I x H Interaction | 1 | 14.46 | 41.16*** |
| Residual | 12 | 0.35 | |

(* Indicates level of significance; *** = 0.5%)

L.S.D. Tests (12 d.f.)

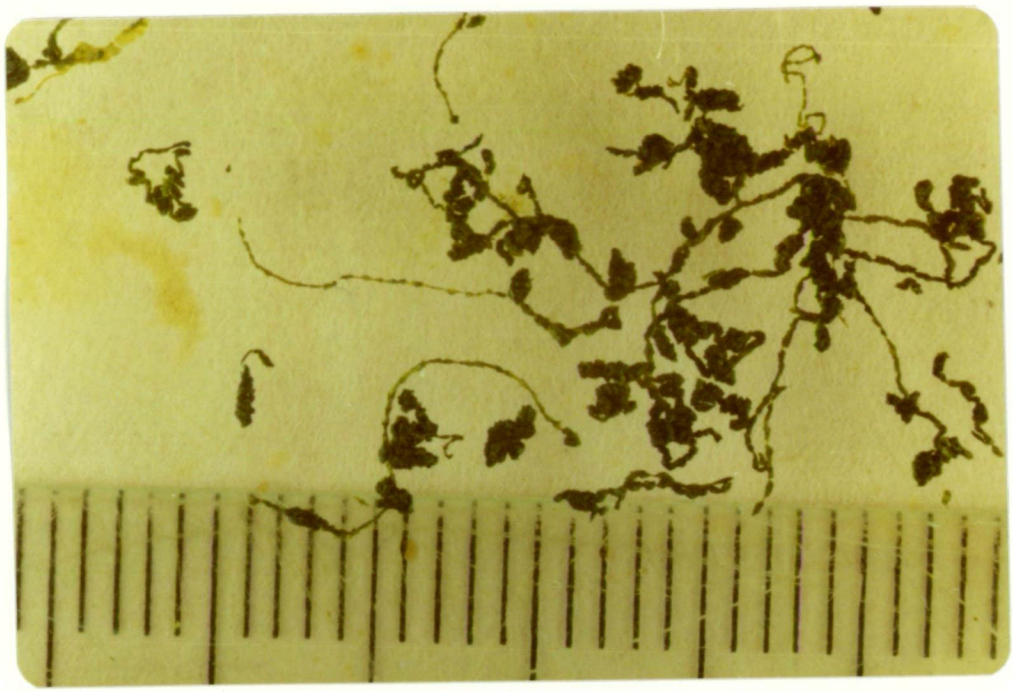
lsd (.05) = 0.91 days; lsd (.01) = 1.28 days

$\bar{x}_a - \bar{x}_b = 4.39$***

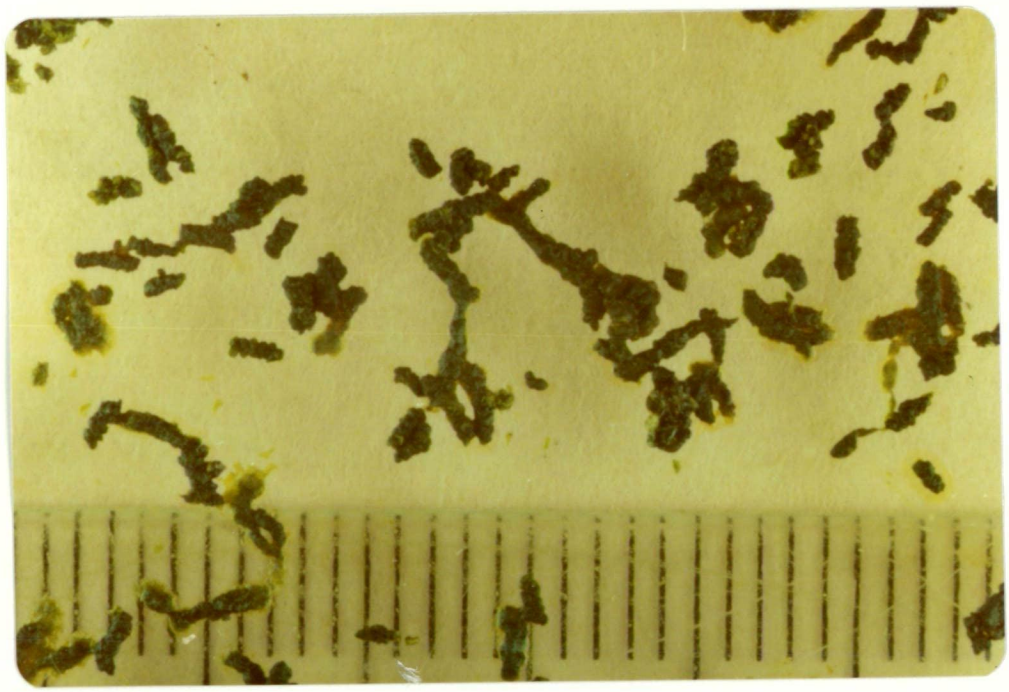
$\bar{x}_c - \bar{x}_d = 0.59$ ns

$\bar{x}_a - \bar{x}_c = 3.03$***

(*** = 0.1%)



(a)



(b)

Fig. 229: Frass excreted by *Chrysophtharta bimaculata* larvae fed (a) *E. dalrympleana* foliage, (b) *E. delegatensis* foliage.

of the larval stages of *C. agricola* on *E. dalrympleana* and on *E. delegatensis*. On *E. delegatensis*, *C. bimaculata* larvae developed significantly faster than larvae of *C. agricola*.

Frass of *C. bimaculata* larvae fed *E. dalrympleana* was excreted in long ribbons with high moisture content, and not as normal discrete pellets (Fig. 229). This indicated an absorptive malfunction.

When surviving larvae were reared through to adults, there was no significant difference between the mean masses of either species reared on either host species (Table 10).

Mean cumulative masses of food consumed for each treatment were plotted against time in Fig. 230. Both species consumed *E. delegatensis* at a faster rate than *E. dalrympleana*. While *C. bimaculata* on *E. delegatensis* had the most rapid rate of consumption, *C. agricola* consumed *E. dalrympleana* more rapidly than did *C. bimaculata*.

Rates of food consumption and gross conversion ratios are shown in Table 11. Means are of four replicate treatment cultures each initially consisting of 25 larvae. Tallies of progressive mortality were kept so that the net consumption of foliage could be calculated at each change of foliage. Statistical differences in the mean gross masses of food consumed between treatments were not significant due to high variance and low replication. Gross conversion ratios (*sensu* Carne 1966a) were obtained by dividing change of mean gross mass of larvae from commencement to conclusion of feeding by mean gross mass of food consumed. Gross conversion ratios for *C. bimaculata* on both host eucalypt species were 0.13, while *C. agricola* had gross conversion ratios of 0.15 and 0.17 on *E. delegatensis* and *E. dalrympleana* respectively.

Table 10.

Mean masses in mg (± S.E.) of adult *C. bimaculata* and *C. agricola* reared as larvae on foliage of *E. delegatensis* and *E. dalrympleana* at 20°C, 16 hours photophase.

| | *E. delegatensis* | *E. dalrympleana* | t test |
|---|---|---|---|
| *C. bimaculata* | 41.25 ± 0.89 (n = 72) | 43.28 ± 0.72 (n = 44) | t = -1.60 ns |
| *C. agricola* | 40.32 ± 0.71 (n = 64) | 42.91 ± 0.58 (n = 78 | t = -1.96 ns |

Table 11.

Mean gross mass of fresh food consumed per larva, mean mass gain per larva, and gross conversion ratios of *C. bimaculata* and *C. agricola* reared on foliage of *E. delegatensis* and *E. dalrympleana* at 20°C, 16 hours photophase.

| Treatment | Mean mass food consumed per larva (mg) ± S.E. (a) | Mean mass gain per larva (mg) ± S.E. (b) | Mean gross conversion ratio (b/a) |
|---|---|---|---|
| *C. bimaculata* - *E. delegatensis* | 414.2 ± 30.9 | 54.3 ± 0.7 | 0.13 |
| *C. bimaculata* - *E. dalrympleana* | 446.8 ± 67.4 | 55.9 ± 2.3 | 0.13 |
| *C. agricola* - *E. delegatensis* | 393.5 ± 27.2 | 58.0 ± 1.4 | 0.15 |
| *C. agricola* - *E. dalrympleana* | 374.3 ± 28.4 | 62.7 ± 1.5 | 0.17 |

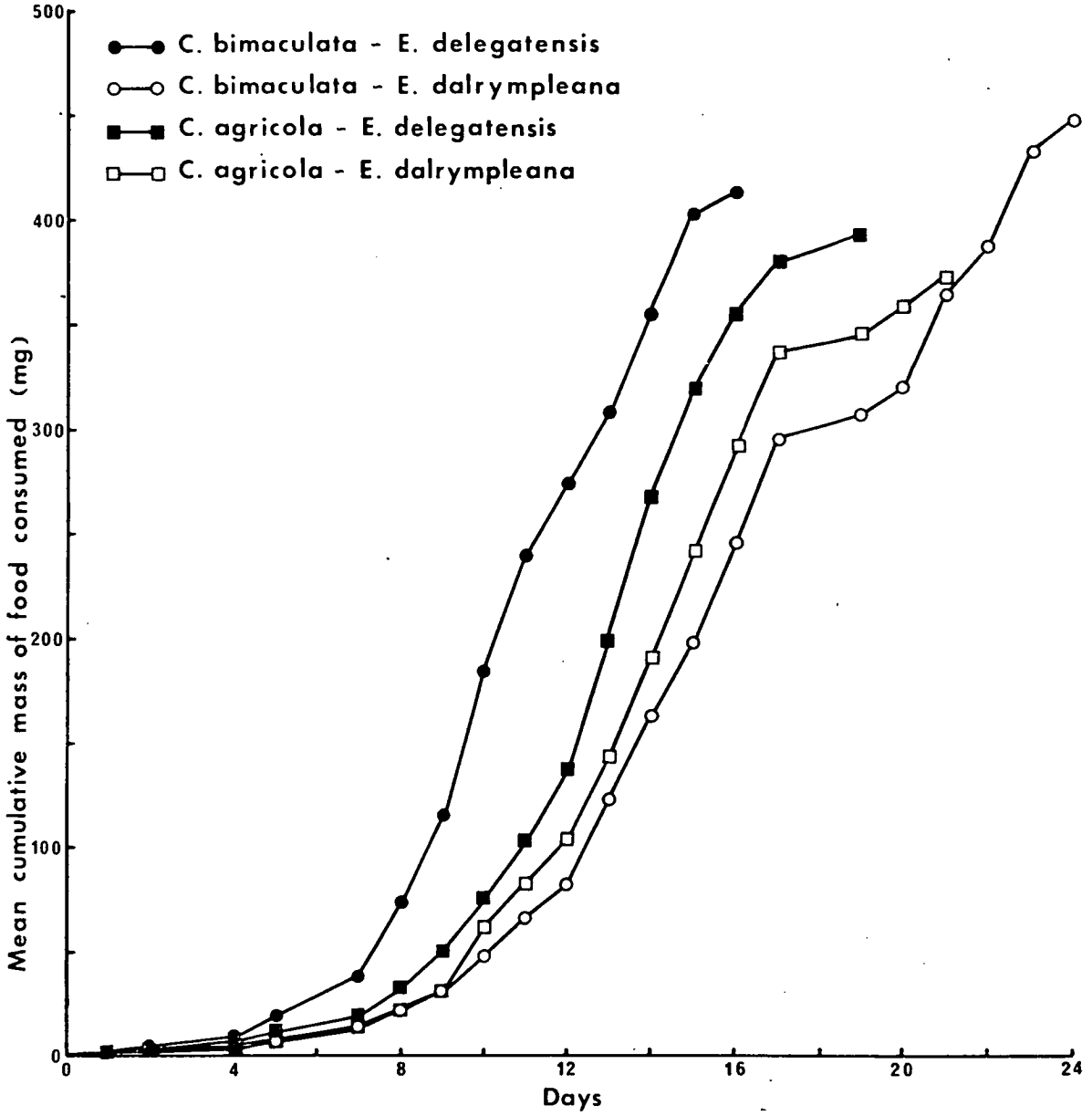



Fig. 230. Larval rates of food consumption.

3.3.6. Survival and rate of growth of larvae of *C. bimaculata* and *C. agricola* on two *Monocalyptus* hosts (*E. delegatensis* and *E. regnans*) and two *Symphyomyrtus* hosts (*E. viminalis* and *E. globulus*) (Appendix 3)

Survival of larvae of both species on each host is shown in Table 12. A significant survival interaction was indicated between the two species and the eucalypt sub-genera, *C. bimaculata* showing a higher survival on the *Monocalyptus* hosts, and *C. agricola* showing a higher survival on the *Symphyomyrtus* hosts. Within sub-genera, there was a significant survival interaction between the two paropsid species and the two *Monocalyptus* hosts, but not the two *Symphyomyrtus* hosts. Survival of *C. agricola* was very low on *E. regnans*, but high on *E. delegatensis*. *C. bimaculata* showed a low survival on both *Symphyomyrtus* hosts.

All comparisons made between durations of larval stages were significant (Table 13), however, with the exception of *C. agricola* on *Monocalyptus* hosts, differences in duration were small. *C. agricola* larvae took nearly twice as long to develop on *E. regnans* as they did on *E. delegatensis*.

3.3.7. Survival and rate of growth of *C. bimaculata* larvae on *Monocalyptus* hosts of the series Obliquae (*E. obliqua*, *E. delegatensis*, *E. regnans* and *E. fastigata*) and the series Piperitae (*E. nitida*) (Appendix 4)

There was no significant difference in survival between larval cultures reared on host foliage of the series Obliquae (Table 14). Survival on foliage of *E. nitida* (series Piperitae) was significantly lower than on some species of series Oblique.

Table 12.

Pupal survival of *C. bimaculata* and *C. agricola* fed as larvae on foliage of two *Monocalyptus* species (*E. delegatensis* and *E. regnans*) and two *Symphyomyrtus* species (*E. viminalis* and *E. globulus*) at 23°C, 16 hours photophase (100 larvae per treatment, initially).

| | *C. bimaculata* | *C. agricola* | Total |
|---|---|---|---|
| (a) *E. delegatensis* | 51 | 74 | 125 |
| (b) *E. regnans* | 66 | 14 | 80 |
| *Monocalyptus* spp. (a + b) | 117 | 88 | 205 |
| (c) *E. viminalis* | 22 | 69 | 91 |
| (d) *E. globulus* | 17 | 56 | 73 |
| *Symphyomyrtus* spp. (c + d) | 39 | 125 | 164 |
| Total | 156 | 213 | 369 |

Interaction $\chi^2$ (*Monocalyptus/Symphyomyrtus*) = 40.03*** (0.1%)

Interaction $\chi^2$ (*E. delegatensis/E. regnans*) = 32.94*** (0.1%)

Interaction $\chi^2$ (*E. viminalis/E. globulus*) = $2.67 \times 10^{-3}$ ns

Table 13.

Durations of larval feeding stage of *C. bimaculata* and *C. agricola* fed foliage of two *Monocalyptus* species (*E. delegatensis* and *E. regnans*) and two *Symphyomyrtus* species (*E. viminalis* and *E. globulus*) at 23°C, 16 hours photophase.

| Treatment | Mean | |
|---|---|---|
| (a) *C. bimaculata* | | |
| *E. delegatensis* | 12.49 ± 0.09 | * |
| *E. regnans* | 12.95 ± 0.13 | |
| *E. viminalis* | 17.32 ± 0.25 | |
| *E. globulus* | 19.82 ± 0.70 | |
| (b) *C. agricola* | | |
| *E. delegatensis* | 14.64 ± 0.10 | |
| *E. globulus* | 16.29 ± 0.15 | |
| *E. viminalis* | 17.01 ± 0.22 | |
| *E. regnans* | 29.50 ± 0.43 | |

*Significance of difference at 5% level using Student-Newman-Keuls test to make multiple comparisons among means based on unequal sample sizes within paropsid species (*a posteriori* tests).

Table 14.

Survival of *C. bimaculata* larvae fed foliage of *E. obliqua*, *E. delegatensis*, *E. regnans*, *E. fastigata* and *E. nitida* at 23°C, 16 hours photophase (25 larvae per replicate).

| | Host | Mean Survival | (± S.E.) | % |
|---|---|---|---|---|
| (a) | *E. obliqua* | 16.25 | ± 2.29 | (65) |
| (b) | *E. delegatensis* | 18.00 | ± 2.08 | (72) |
| (c) | *E. regnans* | 13.75 | ± 1.03 | (55) |
| (d) | *E. fastigata* | 19.50 | ± 1.85 | (78) |
| (e) | *E. nitida* | 9.50 | ± 1.32 | (38) |

Analysis of Variance

| Source of Variance | d.f. | Mean Square | F |
|---|---|---|---|
| Treatments | 4 | 61.83 | 4.84* |
| Residual | 15 | 12.77 | |

(* = 5.0%)

Significance of Differences (Student-Newman-Keuls test)

| | e | c | a | b | d |
|---|---|---|---|---|---|
| 5% level : | | | | | |
| | 9.50 | 13.75 | 16.25 | 18.00 | 19.50 |
| 1% level : | | | | | |

Table 15.

Duration of larval-prepupal stage of *C. bimaculata* fed foliage of *E. obliqua*, *E. delegatensis*, *E. regnans*, *E. fastigata* and *E. nitida* at 23°C, 16 hours photophase.

| Host | Mean duration | (± S.E.) |
|---|---|---|
| (a) *E. obliqua* | 13.70 | ± 0.24 |
| (b) *E. delegatensis* | 12.45 | ± 0.15 |
| (c) *E. regnans* | 13.49 | ± 0.10 |
| (d) *E. fastigata* | 12.96 | ± 0.22 |
| (e) *E. nitida* | 16.34 | ± 0.51 |

Analysis of Variance

| Source of Variance | d.f. | Mean Square | F |
|---|---|---|---|
| Treatments | 4 | 9.10 | 28.44*** |
| Residual | 15 | 0.32 | |

(*** = 0.1%)

Significance of Differences (Student-Newman-Keuls test)

| | b | d | c | a | e |
|---|---|---|---|---|---|
| 5% level : | | | | | |
| | 12.45 | 12.96 | 13.49 | 13.70 | 16.34 |
| 1% level : | | | | | |

The duration of the larval stages was significantly longer on *E. nitida* foliage than on foliage of series Obliquae (Table 15).

4. Discussion

The *Eucalyptus*-defoliating paropsids have evolved a number of protective strategies in their vulnerable leaf-eating habit. Two basic strategies have arisen with regard to oviposition and the feeding habits of the larvae. In species of the genera *Paropsis*, *Chrysophtharta* and *Paropsisterna*, eggs and larvae are exposed on foliage for their full developmental duration, where they are subject to a wide range of climatic conditions, and to avian and insect predation, and parasitoid attack. Eggs and larvae of species of the genera *Trachymela* and *Sterromela* are concealed beneath bark and the larvae emerge to feed nocturnally on foliage. The immature stages of these two genera are thus protected from unfavourable climatic conditions, and from a wide range of predators and parasitoids.These larvae, however, must expend much more energy in the diurnal migration to and from their food source. This results in a greater food requirement and consequent extended developmental period. Since larvae are able to seek refuge under bark from unfavourable weather conditions, a far greater portion of each year is available for larval development.

Adoption of the alternative "exposed" strategy by species of *Paropsis*, *Chrysophtharta* and *Paropsisterna*, has led to the acquisition of a number of adaptive characteristics which include high fertility, short egg and larval developmental times, cryptic or aposematic coloration, gregarious, colonial behaviour of larvae, well-developed defensive glands, and a strong defensive

reaction when disturbed. Not all of these characteristics are shared by all of the "exposed"-strategy species, however, species in which the larvae are strongly gregarious, are usually aposematically coloured and are more fecund. Knerer and Atwood (1973) observed similar combinations of characteristics among spruce-feeding sawfly larvae.

The trend towards "r" selection is greater in species adapted to the "exposed" strategy, and greatest of all in the species with gregarious larvae, where fecundity is high and incubation and duration of larval stages short. The species of *Trachymela* and *Sterromela* which have adopted the "concealed" strategy are at the "K" end of the "r-K" paropsid selection spectrum.

Ovoviviparity, a phenomenon recorded in some northern hemisphere Chrysomelinae (Waloff and Richards 1957), but previously unrecorded among the paropsids, was observed in one species. This was *Chrysophtharta lignea*, an "exposed" strategy species, but with relatively low fecundity and cryptically coloured larvae.

A commonly observed phenomenon among the *Eucalyptus*-defoliating paropsids was the occurrence of several closely related species on a single host eucalypt species. Egg batches of several species of *Chrysophtharta* were observed deposited close to each other, where the emerging larvae were likely to compete for food (Fig. 231). Larvae of two gregarious species were often observed in a single feeding colony (Fig. 232). These observations apparently contradict the "competitive displacement principle" (Grinnell 1904; De Bach 1966). In the two instances documented, i.e. *Chrysophtharta agricola* and

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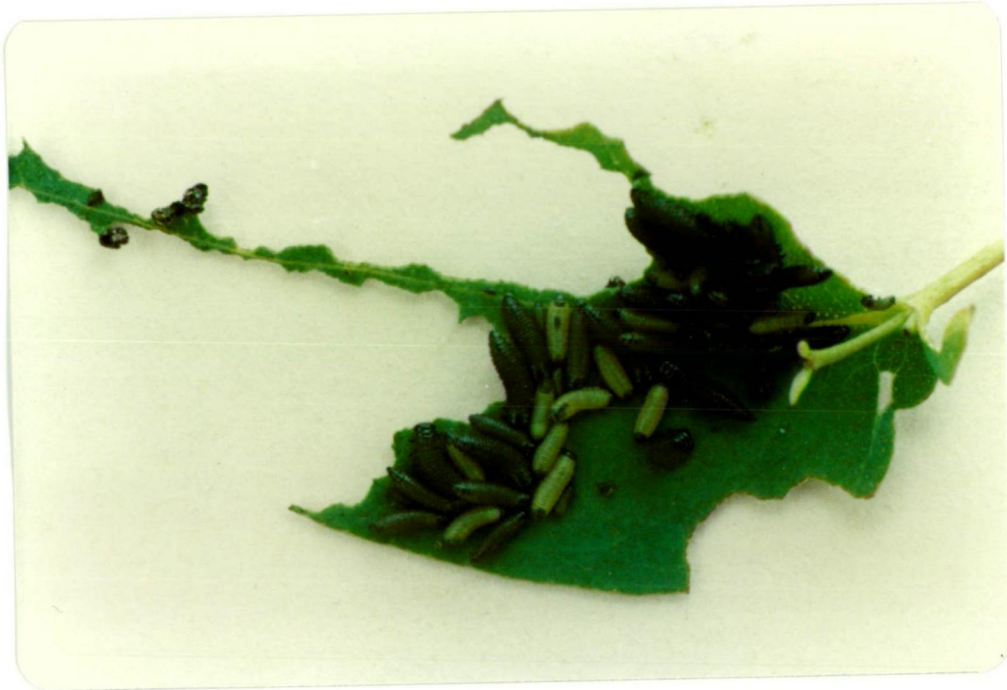

232

Figs. 231, 232: Apparent co-existence of (231) eggs of *Chrysophtharta agricola*, *C. nobilitata* and *C. variicollis* on foliage of *E. dalrympleana*, (232) larvae of *C. agricola* and *C. variicollis* forming one feeding colony on foliage of *E. viminalis*.

*C. variicollis* on *E. gunnii* (Fig. 219), and of *C. nobilitata* and *C. bimaculata* on *E. delegatensis* (Fig. 220), populations of the potentially competitive "competing" species were found to be at least partially separated in time.

*C. agricola* and *C. variicollis* were two very closely related species with similar fecundities and gregarious larval feeding behaviour. It was generally observed (Section III) that *C. variicollis* replaced *C. agricola* on the same, or similar hosts in drier climates. At Ridgley, where spring is normally wet, and summer much drier, conditions favoured *C. agricola* early in the season. *C. variicollis* adults only became abundant on the host trees later, in the drier summer conditions. This phenological adaptation enabled two univoltine species to utilize succeeding foliage flushes of a single host species in one season, with minimal competition.

*C. bimaculata* and *C. nobilitata* were less closely related, the former species having a high fecundity and gregarious larvae, and the latter species having a much lower fecundity and larvae which were solitary. In the short season available for "exposed" strategy species in "Surrey Hills", *C. nobilitata* was adapted to oviposit and feed early in the season on very young leaflets of *E. delegatensis*, which were not attractive to *C. bimaculata*. *C. bimaculata* adults did not become abundant on *E. delegatensis* foliage until it was nearly fully expanded, when massive oviposition occurred. Again, competition between the two paropsid species on the same host was minimal.

The *Eucalyptus*-defoliating paropsids showed very different host-plant relationships to the chrysomeline defoliators of

*Alnus*, *Populus* and *Salix* in North America. There, Brown (1956, 1959) found that within a genus, species were isolated on different host species, and in the absence of clearly defined morphological characteristics, it was possible to identify these species on the basis of the host tree on which they were collected.

Eucalypts generally grow together naturally in stable associations of two or three relatively unrelated species. It was commonly observed that although several closely related paropsid species frequently occurred on the same host eucalypt species, a number of species showed evidence of host specificity at any locality where there was a choice of potential hosts. This was in agreement with observations made by Burdon and Chilvers (1974) and Morrow (1977) in mainland S.E. Australian localities.

The two most abundant paropsid species in a three-species mixed eucalypt stand sampled at regular intervals throughout one season, showed distinct host preferences. These species, *C. bimaculata* and *C. agricola*, were closely related, both having adopted the "exposed" strategy and having gregarious larvae and high fecundities. They also had closely synchronized phenologies. Although these two species showed strong host preferences in the field, their distributions were not totally restricted to their preferred hosts. Adults, eggs and larvae of *C. agricola* occurred on *E. delegatensis*, the preferred host of *C. bimaculata*, but only adults of *C.bimaculata* occurred on *E. dalrympleana* which was the preferred host of *C. agricola*.

Preferences exhibited by *C. bimaculata* and *C. agricola* in the field were retained in a cage trial, when field collected

adults were offerred a choice of foliage of *E. delegatensis* and *E. dalrympleana* for oviposition. In this situation, however, oviposition of both species on their non-preferred hosts was recorded. Since larvae of "exposed" strategy species are incapable of substantial migration, the adult female bears the onus of selecting the most suitable host.

Larval feeding trials of *C. bimaculata* and *C. agricola* larvae fed foliage of *E. delegatensis* and *E. dalrympleana* indicated that while *C. bimaculata* larvae suffered a physiological disability on foliage of the non-preferred host, *E. dalrympleana*, this was not the case with *C. agricola*. *C. agricola* developed as well on *E. delegatensis* as on the preferred host, *E. dalrympleana*.

In his determination of the gross conversion ratio of larvae of *Paropsis atomaria*, Carne (1966b) suggested that this ratio might differ considerably from those which would be obtained if the species of foliage was varied. The ratio of 0.20 obtained for *P. atomaria* larvae fed foliage of *E. blakelyi*, was higher than ratios obtained for *C. bimaculata* and *C. agricola* in the present study, indicating that *P. atomaria* was a more efficient feeder than either species of *Chrysophtharta*. In the present study, the ratio for *C. bimaculata* on both hosts was 0.13, while the ratios for *C. agricola* were 0.15 and 0.17 on *E. delegatensis* and *E. dalrympleana* respectively. This indicated that *C. agricola* was a more efficient feeder than *C. bimaculata*.

Southwood *et al.* (1974) proposed that the adventitious phytophagous insects which colonize transient habitats are selected for maximal food intake rather than for their ability to utilize food efficiently. This means that highly "r" selected

species are favoured in such situations where rapid population growth is at a premium, rather than the conservation of food resources. Although a less efficient feeder, *C. bimaculata* developed significantly faster than *C. agricola* on *E. delegatensis*. Since *C. bimaculata* was therefore a more highly "r" selected species than *C. agricola*, it had a selective advantage on *E. delegatensis*. *C. agricola* had therefore adapted to a host (*E. dalrympleana*) which was as suitable to it as *E. delegatensis*, but on which it did not face competition from a more highly "r" selected species. Carne (1966a) similarly found in laboratory feeding trials, that foliage of some eucalypt species on which *P. atomaria* larvae rarely or never occurred in the field were as suitable in the laboratory, as the field preferred hosts.

When feeding trial experimentation with larvae of *C. bimaculata* and *C. agricola* was extended to foliage from a wider range of eucalypt species, a more complex pattern of host suitability emerged. Performance of *C. bimaculata* larvae was better, in terms of survival and speed of development, on foliage of *E. delegatensis* and *E. regnans* than on *E.viminalis* and *E. globulus*. According to the classification of Pryor and Johnson (1971), the former two eucalypt species were placed in the sub-genus *Monocalyptus*, series Obliquae, while the latter two species belonged to the sub-genus *Symphyomyrtus*, series Viminales. *C. agricola* larvae performed better on *E. delegatensis* than on either of the two *Symphyomyrtus* species, both species on which it was frequently collected. However, survival of *C. agricola* larvae on *E. regnans*, the other *Monocalyptus* species, was very low, and larval duration of survivors was approximately twice as long as on *E. delegatensis*.

*C. agricola* larvae suffered obvious physiological disabilities on *E. regnans*, as did *C. bimaculata* larvae on *Symphyomyrtus* hosts. If the essential oils of eucalypts have a role in protecting them from defoliation by paropsids, then it is possible that the oil eudesmol, which is present in foliage of *E. regnans* but absent from *E. delegatensis* (Penfold and Willis 1961), may deter *C. agricola*.

Little difference was seen between the performance of *C. bimaculata* larvae on four species of the subgenus *Monocalyptus*, series Obliquae. One of the species included was *E. fastigata*, a species not native in Tasmania, and foliage of which has been reported as inadequate to rear larvae of *Paropsis charybdis* in New Zealand (Styles 1970; Steven 1973). This species was just as suitable for *C. bimaculata* as were the three natural hosts, *E. delegatensis*, *E. regnans* and *E. obliqua*. *E. nitida* (*Monocalyptus*, series Piperitae) which was also included in the trial, was less suitable for *C. bimaculata* larvae, although both adults and eggs have been collected from it in the field.

Therefore, the inter-specific relationships among the *Eucalyptus*-defoliating paropsids are seen to consist of a mosaic of strategies which permit the survival and "co-existence" of many species in a multiplicity of niches in a relatively harsh environment. In this study, no case of true "co-existence" (De Bach 1966) was observed on a single host. The most highly "r" selected species are those which have adopted the "exposed" strategy and in which the larvae feed in gregarious groups. At the "r" end of the "r-K" spectrum of selection, host

preference in the field among species is determined by a combination of factors which include relative "r" selection of species and inherent host favourability.

# SECTION V - LIFE HISTORY AND POPULATION ECOLOGY OF *CHRYSOPHTHARTA BIMACULATA*

## 1. Introduction

The life history and population ecology of *C. bimaculata* was investigated in N.W. Tasmania. The species occurred in outbreak numbers on young *E. delegatensis* regeneration in the "Surrey Hills" property of Associated Forest Holdings Pty. Ltd. at the commencement of the study in 1973.

Aspects of the life history were studied in the field, in insectaries and in the laboratory. Limited studies of the behaviour of some of the major natural enemies were undertaken.

A detailed programme of population sampling was undertaken over a period of three seasons at sites in "Surrey Hills" and at East Ridgley. This sampling was discontinued when populations declined to a level where sampling of a desirable precision became impracticable. Partial population budgets were constructed for immature populations at East Ridgley in two successive seasons (1974/75 and 1975/76) and for one study area (Bunkers Thinned) in "Surrey Hills" in the 1974/75 season.

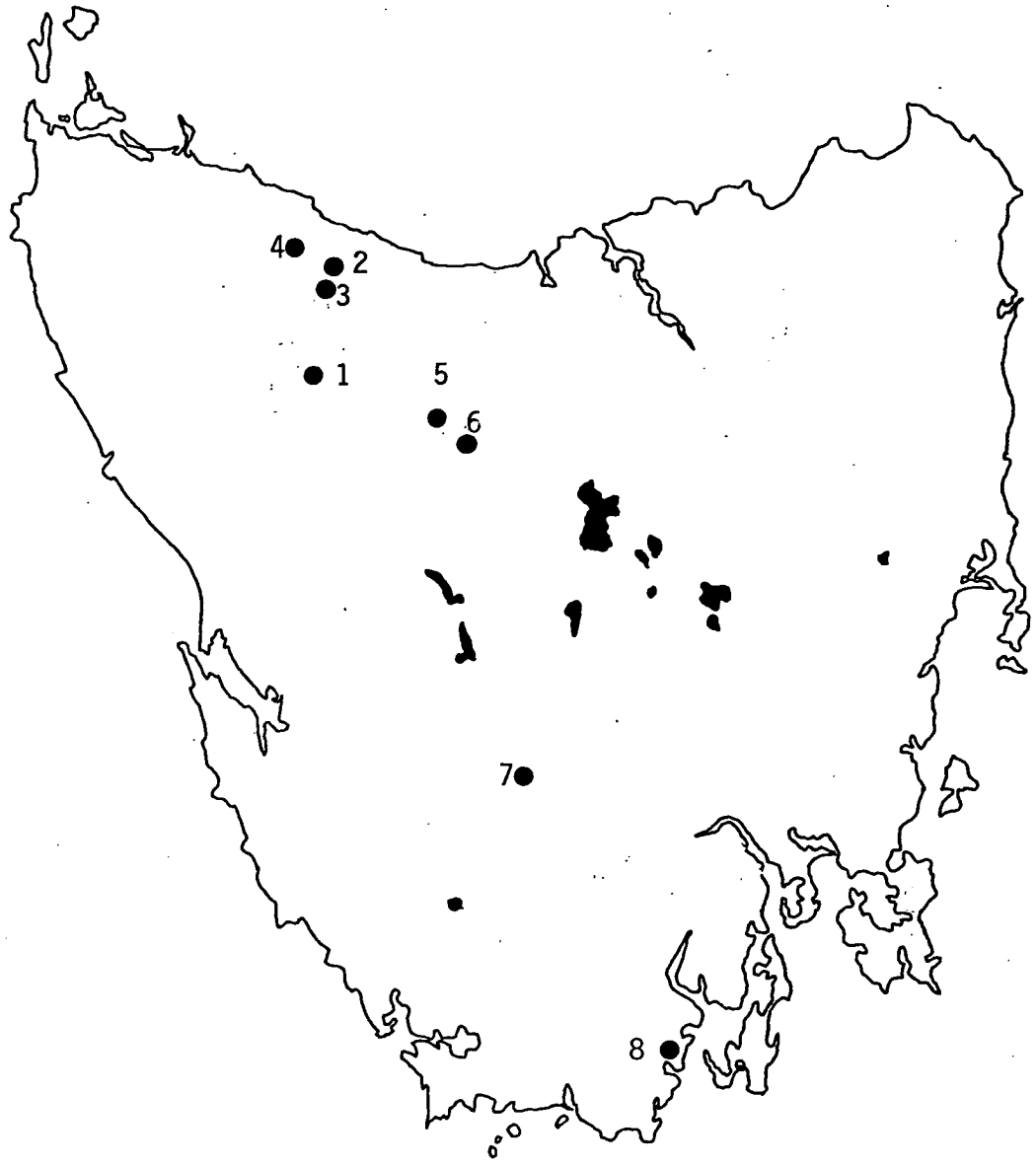


Fig. 233. Sites throughout Tasmania where observations were made on *Chrysophtharta bimaculata* populations: 1, "Surrey Hills"; 2, Ridgley; 3, Highclere; 4, Inglis R. Valley; 5, Mersey Valley; 6, Walls of Jerusalem; 7, Florentine Valley; 8, Southern forests.

## 2. Materials and Methods

### 2.1. Study areas

Aspects of the life history and population dynamics of *C. bimaculata* were studied in the East Ridgley and "Surrey Hills" areas of N.W. Tasmania (Fig. 233) in successive summers from 1973/74 to 1977/78.

#### 2.1.1. East Ridgley

The study area (Figs. 234, 235) was located in a eucalypt plantation at an altitude of 340 m on soils of mixed basaltic and granitic origin. The average annual rainfall was 1300 mm. The area was demarcated by cleared pasture to the north, an advanced natural regeneration stand of *E. obliqua* with an understorey of wet sclerophyll mixed scrub to the west, and young *E. obliqua* and *E. delegatensis* plantations to the east and south, respectively. The study site was located in a small block of *E. regnans* planted in 1971 and in the two to five metre height class in the spring of 1974. The block consisted of eleven rows of approximately 35 trees per row planted at a three by three metre spacing. The ground cover was mainly densely matted blackberry (*Rubus fructicosus* L.) vines.

#### 2.1.2. Surrey Hills

Two study sites, at which there was evidence of paropsid activity, were selected in the Bunkers Road area of "Surrey Hills" (Figs. 236, 237, 238). These were known as "Bunkers Thinned" and "Bunkers Grass". The vegetation at Bunkers Thinned consisted of a stand of 1.5 to 3 m high *E. delegatensis* regeneration with a sparse ground cover and shrub understorey consisting mainly of

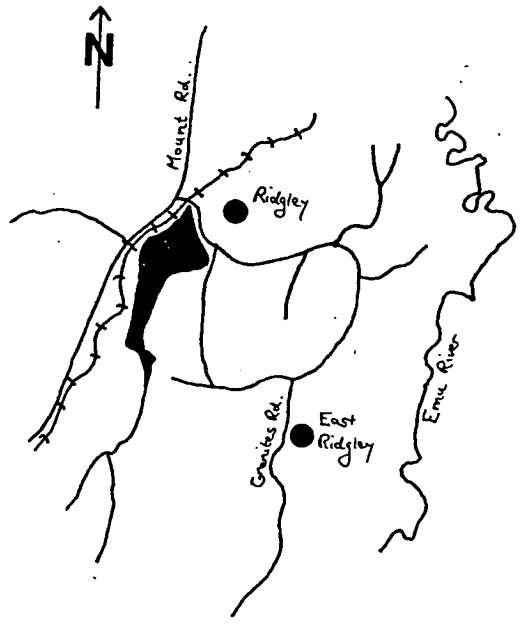


Fig. 234. Locality map of East Ridgley study site.
(Scale: 1 cm = 1 km)

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Fig. 235: East Ridgley study site photographed December 1975 showing plantation *E. regnans* on which sampling for *Chrysophtharta bimaculata* was conducted.

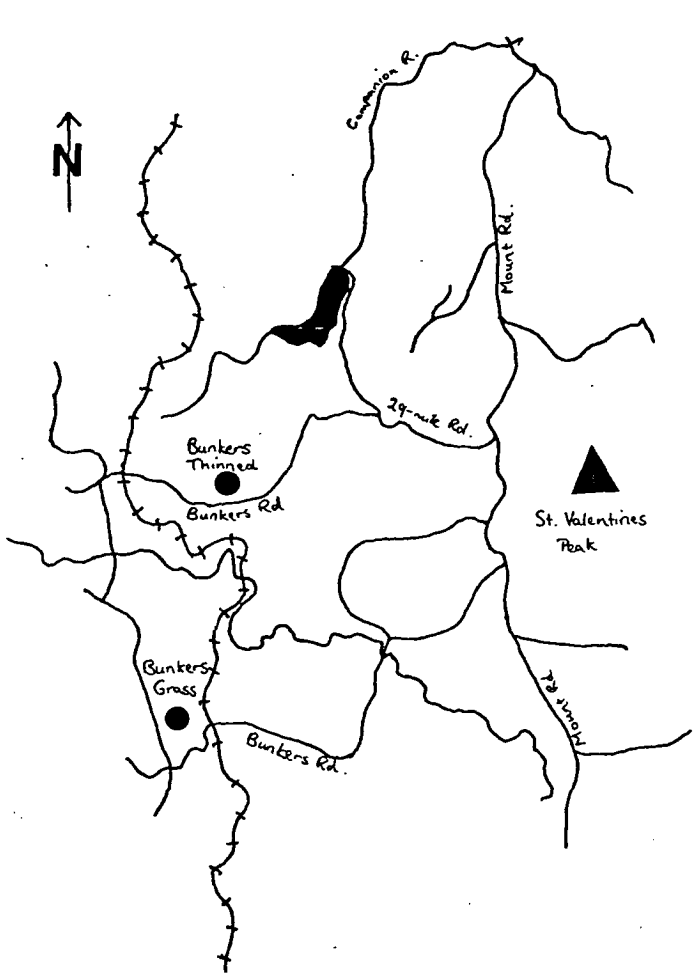


Fig. 236. Locality map of "Surrey Hills" study sites, "Bunkers Thinned" and "Bunkers Grass". (Scale: 1 cm = 1 km)

237

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Figs. 237, 238: Study sites at Bunkers Road, "Surrey Hills", photographed March 1974 showing regeneration *E. delegatensis* on which sampling for *Chrysophtharta bimaculata* was conducted, (237) "Bunkers Thinned"; (238)"Bunkers Grass".

*Nothofagus cunninghamii* (Hook.) Oerst. (Antarctic beech), *Drimys lanceolata*(Poir.) Baill. (native pepper), *Zieria arborescens* Sims. (stinkwood), *Telopea truncata* (Labill.) R. Br. (waratah), *Phyllocladus asplenifolius* (Labill.) Hook. f. (celery-top pine), *Cyathodes parvifolia* R. Br. (pink mountain berry) and *Acaena novae-zelandiae* Kirk (buzzy). A stand of 1.5 to 4 m high *E. delegatensis* regeneration on a tussock-grass plain constituted the main vegetation at Bunkers Grass. The dense ground cover consisted mainly of *Poa labillardieri* Steud. (silver tussock grass), with some low shrubs including *Cyathodes parvifolia* R. Br. and *Lomatia tinctoria* R. Br. (guitar plant).

2.2. Meteorological data

Monthly rainfall figures for Burnie since 1887 were used to indicate past rainfall trends for the north-west region of Tasmania. Daily rainfall records were maintained at Ridgley and at Guildford.

Thermographs were established in standard Stevenson screens at Ridgley on 22.x.1974, and at Bunkers Thinned and Bunkers Grass on 18.i.1974. Continuous temperature records were maintained until the conclusion of the study.

2.3. Sampling methods

The selection of the shoot sample unit as the quantitative unit for the study of abundance of immature stages was discussed in section IV.2.2. Preliminary sampling was conducted in the first season of the study (1973/74) to gain an overall impression of the phenology and abundance of *C. bimaculata*. The method used by Carne (1966a) for recording populations of *Paropsis atomaria* was followed. This system, however, was found to be inadequate for detailed population measurement, because of the changing dominance

of shoots through the season, and a system of destructive sampling was developed, similar to the method used by Madden and Bashford (1977) for sampling immature stages of the moth *Chlenias* sp. Intensive population sampling using this method was undertaken in the 1974/75 season at East Ridgley and at Bunkers Thinned, and in the 1975/76 season at East Ridgley only. Sampling was abandoned at Bunkers Grass in 1974/75, in "Surrey Hills" generally in 1975/76 and altogether, thereafter, due to very low to virtually non-existent, populations. Under these conditions it was not practically possible to achieve a sample error within ten percent of the sample mean.

In the 1976/77 and 1977/78 seasons, adult *C. bimaculata* were collected at regular intervals from study areas, their colour phase recorded, and the ovaries of the females dissected out and scored for development. Collections of larvae of all instars were made at regular intervals, and parasites bred out in the laboratory.

### 2.3.1. Preliminary sampling, 1973/74 season

The Bunkers Thinned and Bunkers Grass study sites were chosen for population studies because large populations had been observed in these sites in the previous season (1972/73)(D. de Boer, *pers. comm.*). Six shoots were tagged on each of ten trees and sampling was carried out at frequent intervals as described in section IV.2.2.

Numbers of each stage were recorded at each time of sampling, with the exception that second and third instar larvae were recorded as a single stage due to difficulty in identifying these instars in large feeding groups. Numbers of predators, and the numbers of larvae bearing visible parasitic tachinid eggs were also recorded.

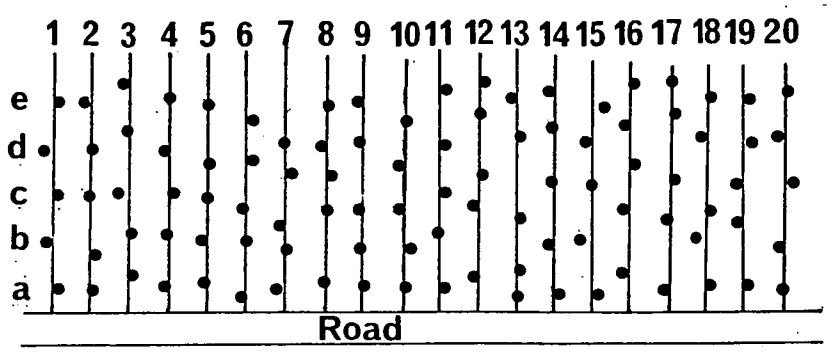
It was found necessary to re-tag shoots in mid-season. This was because shoots which were dominant early in the season received more defoliation earlier, and by mid-season, previously suppressed shoots had assumed dominance and were attracting more beetle activity. Dominant shoots at these two study sites were randomly re-tagged on the same sample trees in mid-January.

Estimates of sample variance were made on population data of *C. bimaculata* obtained at Bunkers Thinned and Bunkers Grass (Appendix 5). Standard errors of mean peak population samples of each of the immature stages sampled at each site were calculated. Numbers of samples (shoots) required to give standard errors of 10 percent of the mean population per shoot were evaluated in each case, with respect to the two parameters of shoot occupancy, and numbers of each stage occurring on occupied shoots. With respect to shoot occupancy, the number of shoots required to give a ten percent standard error at peak population level varied between 54 shoots for eggs and 900 shoots for fourth instar larvae. The numbers of occupied shoots required to give a ten percent standard error of the mean population per occupied shoot at peak population level varied between 36 shoots for fourth instar larvae and 115 shoots for second and third (mid) instar larvae.

### 2.3.2. Destructive sampling technique

The system of destructive sampling involved the ranking of a large number of shoots in the field for the presence or absence of stages, and removal of a sub-sample of occupied shoots for detailed analysis in the laboratory.

A number of transects were marked out in each study site at approximately ten metre intervals, running perpendicular to access

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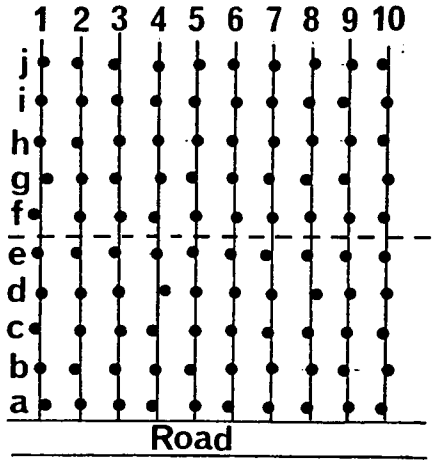


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Figs. 239, 240. Study area plans showing sampling transects and sampling points of

(239) Bunkers Thinned, and

(240) East Ridgley.

roads, and "sampling points" were located on each transect (Figs. 239, 240). Sampling points consisted of either a single tree or group of trees. At Bunkers Thinned, twenty transects were established, with five sampling points on each transect, and at East Ridgley, ten transects were established, each with ten sampling points. At East Ridgley, the sample points corresponded with the rows of the plantation. Selected sampling points were sampled at each sampling date, according to the plan shown in Table 16. This regular rotation of sampling points within each transect ensured that the whole study site was covered in a relatively uniform manner at each sampling date while sampling at each sampling point on only every fifth sampling date favoured for minimal disturbance of the study area.

At each sampling point, ten to twenty-five randomly selected shoots were examined for the presence or absence of immature stages of *C. bimaculata*, and the first three occupied shoots removed for detailed counts of numbers. If three shoots out of ten were not occupied, sampling was continued until three occupied shoots were encountered. If three occupied shoots were not encountered in the examination of twenty-five shoots, sampling at that sampling point was discontinued. Hence 200 to 500 randomly selected shoots were ranked for occupancy, and a sub-sample of up to 60 occupied shoots were removed for counts of all stages, and residual egg clusters. This procedure resulted in a very large number of shoots being examined both early and late in the season, but in mid-season, when shoot occupancy was highest, less shoots were examined in order to obtain the requisite three occupied shoots from each sampling point. Counts of adult *C. bimaculata*, and of known insect predators were made on the

Table 16. Sampling plan of destructive sampling technique on successive times of sampling at Bunkers Thinned and East Ridgley study sites.

| Sampling time | Sampling points sampled on successive times of sampling |
|---|---|
| | Bunkers Thinned |
| 1st | 1a, 2b, 3c, 4d, 5e, 6a, 7b, 8c, 9d, 10e, 11a, 12b, 13c, 14d, 15e, 16a, 17b, 18c, 19d, 20e. |
| 2nd | 1b, 2c, 3d, 4e, 5a, 6b, ..... etc. |
| 3rd | 1c, ..... etc. |
| 4th | 1d, ..... etc. |
| 5th | 1e, ..... etc. |
| 6th | 1a, ..... etc. |
| 7th | etc. |
| | East Ridgley |
| 1st | 1a, 1f, 2b, 2g, 3c, 3h, 4d, 4i, 5e, 5j, 6a, 6f, 7b, 7g, 8c, 8h, 9d, 9i, 10e, 10j. |
| 2nd | 1b, 1g, 2c, 2h, 3d, 3i, 4e, 4j, 5a, 5f, 6b, 6g, ..... etc. |
| 3rd | 1c, ..... etc. |
| 4th | 1d, ..... etc. |
| 5th | 1e, ..... etc. |
| 6th | 1a, ..... etc. |
| 7th | etc. |

shoots in the field.

The sampling system was modified during the 1975/76 season to decrease sample variance. Immature stages occurring on the foliage were sub-divided into three groups, *viz.* eggs, first to third instar larvae, and fourth instar larvae. The sampling procedure described above was adopted for each of these three stages, individually, which meant that the accuracy with which each stage was sampled was not necessarily determined by the abundance of the most abundant stage. Shoot occupancy data was recorded in the field, on a specially devised sheet (Fig. 241) and numbers data were also entered after assessment in the laboratory.

Population estimates made at East Ridgley in 1975/76 were converted to absolute estimates. This required an estimate of the average number of shoots per unit area in the study site, throughout the season. Five shoot units were tagged on one tree at each of twenty sampling points early in the season, giving a total of 100 tagged shoots. At the conclusion of activity for the season, the total number of shoots into which the initial 100 tagged shoots had developed, were counted. A median value was then estimated, approximating to the number of shoots mid-season (Appendix 6). At the conclusion of activity, the total numbers of shoots on each of the trees bearing tagged shoots were counted, and the numbers of shoots per tree in mid-season were estimated. The mean number of shoots per tree at mid-season, was then multiplied by tree density in the study area to give a mean number of shoots per unit area. Population estimates measured as numbers per shoot, were expressed in the absolute unit of numbers per square metre (of ground surface).

Fig. 241. Sample sampling data sheet showing spaces for recording occupancy in field of 25 shoots for eggs, 1st to 3rd instar larvae (L1-3), 4th instar larvae (L4), adults and predators (Cl.me. = *Cleobora mellyi*) (SO = shoots occupied, SS = shoots sampled, TSS = total shoots sampled); and for recording numbers data in laboratory (Tpr = total predated; Tpa = total parasitization, pae = parasitoids emerged; TB = total batches; TE = total eggs; TL = total larvae; te = no. of larvae with tachinid eggs; tem = tachinid parasitoids emerged; bem = braconid parasitoids emerged; X = mortality source unknown; Pu = no. pupated).

Study site East Ridgley Date 8. xii. 75

Transect 7 Sampling point 9

Shoot occupancy data

| | Eggs | | | L1-3 | | | L4 | | | Adults | | | Pred. | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | ✓ | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | | |
| 3 | | | | | | | | | | | | | | | |
| 4 | | | | | | | | | | | | | | | |
| 5 | | ✓ | | ✓ | | | | | | | | | | | |
| 6 | ✓ | | | | | | | | | | | | | | |
| 7 | | | | ✓ | | | | | | | | | | | |
| 8 | | | | ✓ | | | | | | | | | | | |
| 9 | | | | | | | | | | | | | 1A Cl. me. | | |
| 0 | ✓ | | | ✓ | | | | | | | | | | | |
| SO | 3 | | | 5 | | | | | | | | | | | |
| SS | 15 | | | 10 | | | | | | | | | | | |
| TSS | 15 | | | | | | | | | | | | | | |

Numbers data

| Eggs | Nos./ batch (predated) | Tpr | Tpa | pae | TB | TE |
|---|---|---|---|---|---|---|
| | 39(20), 30(22), 20(18). | 60 | 29 | 19 | 3 | 89 |

| L1 | TL | te | L2 | TL | te | L3 | TL | te |
|---|---|---|---|---|---|---|---|---|
| | 21 | 2 | | 27 | 2 | | | |

| L4 | TL | te | tem | bem | X | Pu |
|---|---|---|---|---|---|---|
| | | | | | | |

### 2.3.3. Estimating pupal mortality

Pupal mortality was estimated at East Ridgley in 1975/76 by placing prepupae, collected from adjacent to the study site in metal cylinders 13 cm high and 28 cm in diameter (Fig. 242), similar to those described by Styles (1970). These cylinders were open at the bottom and were driven approximately eight centimetres into the ground. The top was covered with fine wire mesh after 25 prepupae had been placed on the soil in each cylinder. Cylinders were established beneath crown projections of trees at sampling points 1a, 2b, 3c, 4d, 5e, 6f, 7g, 8h, 9i, and 10j, such that there were ten cylinders and a total of 250 prepupae. This procedure was carried out concurrently with the natural occurrence of the fourth instar larvae, and cylinders were established beneath trees just prior to drop and the entry of fully fed fourth instar larvae into the soil.

## 2.4. Laboratory techniques

### 2.4.1. Destructive sampling technique

Occupied shoots that were sub-sampled for counts of numbers of each stage were collected and placed in plastic bags. One bag was used for all sub-sampled shoots from each sampling point. Bagged shoots were transported to the laboratory in a pre-cooled "Eski" container, to retard development after field sampling. Shoots were then stored at $4^{o}C$ for up to 24 hours, until numerical counts could be made. Data were entered on the sampling sheets as shown in Fig. 241.

Numbers of egg batches and eggs per batch were counted. The numbers of predated eggs were estimated from chorion remains or


Fig. 242: Cylinder for measuring pupal mortality at study site.

from foliage attachment marks. Parasitized eggs were recognised by the presence of an oviposition puncture mark, usually towards one end of the egg, and/or by the development of a band of black pigmentation within the egg. In the rare instance where entire egg batches had either been predated or parsitized, an estimate of their age was made by comparing the relative separation of eggs or their remains in the raft, due to leaf expansion, and comparing this with healthy egg batches on similarly aged leaves. In this way it was possible to estimate the total number of eggs, assuming no predation or parasitization. This procedure was important in the estimation of the total egg recruitment (Section V.2.5.2.). Parasitized egg batches were held in petri dishes in the laboratory, and emergent parasitoids were collected for identification.

Larval numbers in each instar were counted, and numbers of larvae bearing one or more parasitic tachinid eggs on the cuticle were also assessed. Fourth instar larvae were reared through to prepupae, when they were placed in pupation cells. Plastic link matting was used in 1974/75, and gelatin capsules were used in 1975/76. The eventual fate of each fourth instar larva was recorded, and emerging parasitoids collected for identification.

### 2.4.2. Oviposition trial

A number of adults were collected from foliage at East Ridgley, 1976/77, before field oviposition had commenced. Sixty-one females were weighed, and five large (100-120 mg), five medium (70-90 mg) and five small (40-60 mg) females were selected for an oviposition trial. Appropriately sized males were matched with females in each size class, and individual pairs placed in petri dishes on fresh *E. regnans* foliage, and held at 24$^{o}$C and with 16 hours photophase.

The foliage was changed every 2-3 days when the eggs were counted. Males within each size category were transferred successively to each dish to minimize the effect of the possibility of a sterile male. Dead males were replaced, and each culture maintained until the female died.

2.4.3. Temperature-developmental curves of eggs and larvae

The incubation periods and developmental times of eggs and larvae of *C. bimaculata* at constant temperatures of 8°C, 15°C, 20°C, 24°C and 27°C were determined by R. Greaves (1966 and unpubl. information). An unsuccessful attempt was made to replicate larval development curves at constant temperatures on *E. regnans* and *E. delegatensis* foliage. At the commencement of the 1974/75 season, egg batches were collected in the field at East Ridgley and sent to the University of Tasmania in Hobart. Foliage of *E. regnans* and *E. delegatensis* was collected from Mt. Wellington, but after normal hatch survival of larvae on both species was so low that no reliable estimate assessment of rates of development could be obtained. Consequently, the data of Greaves (*loc. cit.*) (Appendix 7) was, with permission, utilized.

Exponential curves (Table 17) were fitted to the data for eggs, each larval instar (feeding stage only of fourth instar), and first and second instars combined, so that mean rates of development in the field could be derived.

2.4.4. Sex ratio and physiological status of adults

Collections were made of adult *C. bimaculata* at approximately weekly intervals throughout the 1976/77 season, from East Ridgley. Adults were aged, sexed, and classified with respect to colour phase.

Table 17. Exponential curve fit of form $y = ae^{bx}$ (where y is developmental time of stage in days, and x is temperature in degrees Celsius) to temperature-developmental data* for eggs and larvae of *C. bimaculata* reared at constant temperature on foliage of *E. regnans*.

| | a | b | $r^2$ |
|---|---|---|---|
| Eggs | 21.41 | -0.06 | 0.99 |
| L1 | 23.91 | -0.09 | 0.99 |
| L2 | 18.44 | -0.09 | 0.96 |
| L1-2 | 42.14 | -0.09 | 0.996 |
| L3 | 17.45 | -0.08 | 0.94 |
| L4 | 29.73 | -0.10 | 0.96 |

*Raw data after R. Greaves (1966, unpubl. information).

The character of hind-wing coloration used by Dunn (1951) to age *Leptinotarsa decemlineata* beetles was found useful in separating overwintered, reproductively mature *C. bimaculata* adults from newly emerged, teneral adults. Mature adults had mauve-coloured hind-wings, while in teneral adults the hind-wings were uncoloured (Fig. 243).

The ovaries of females were dissected out and classified with respect to colour of calyx and condition of ovarioles. A red calyx region was an indication of sexual maturation of ovaries. Ovarian development was ranked into four categories on the basis of Davies' (1966) classification (under controlled conditions of 25$^{o}$C, 16 hours photophase); undeveloped, days 1-3; +, days 4-6; ++,days 708; and +++ (fully developed) day 9 onwards.

Populations of *C. bimaculata* were established in outside insectaries (covered with 2 mm nylon mesh) at Ridgley on *E. delegatensis*. During the 1976/77 season, observations were made on adult beetles with respect to colour phase, and ovarian condition of females.

### 2.4.5. Predation trials

Trials were conducted in plastic petri dishes at 23$^{o}$C and 16 hours photophase. The predators in the trials were the larvae and adults of the coccinellid *Cleobora mellyi*, and the prey were the eggs and larvae of *C. bimaculata*. Mature, field collected adults and laboratory hatched larvae of *Cl. mellyi* were used in trials. All prey were field collected. In adult feeding trials, mating pairs were held separately in petri dishes and fed a surfeit of prey. Larval feeding trials were conducted with single *Cl. mellyi* larvae due to the cannibalistic habits of this species.

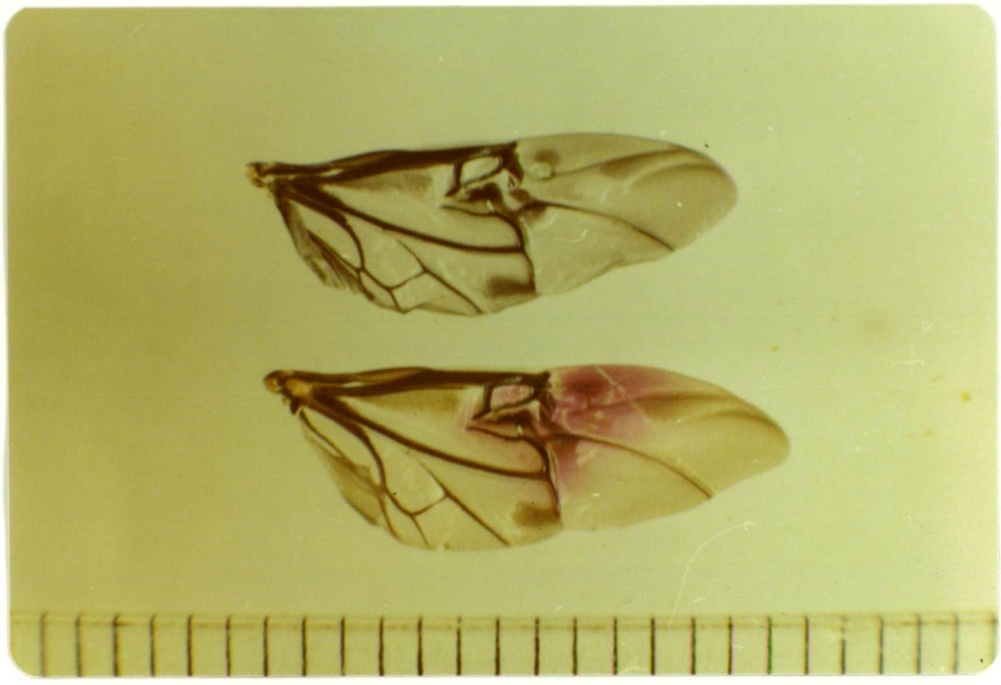

Fig. 243: Hind wings of *Chrysophtharta bimaculata*, top, teneral adult, bottom, mature overwintered adult.

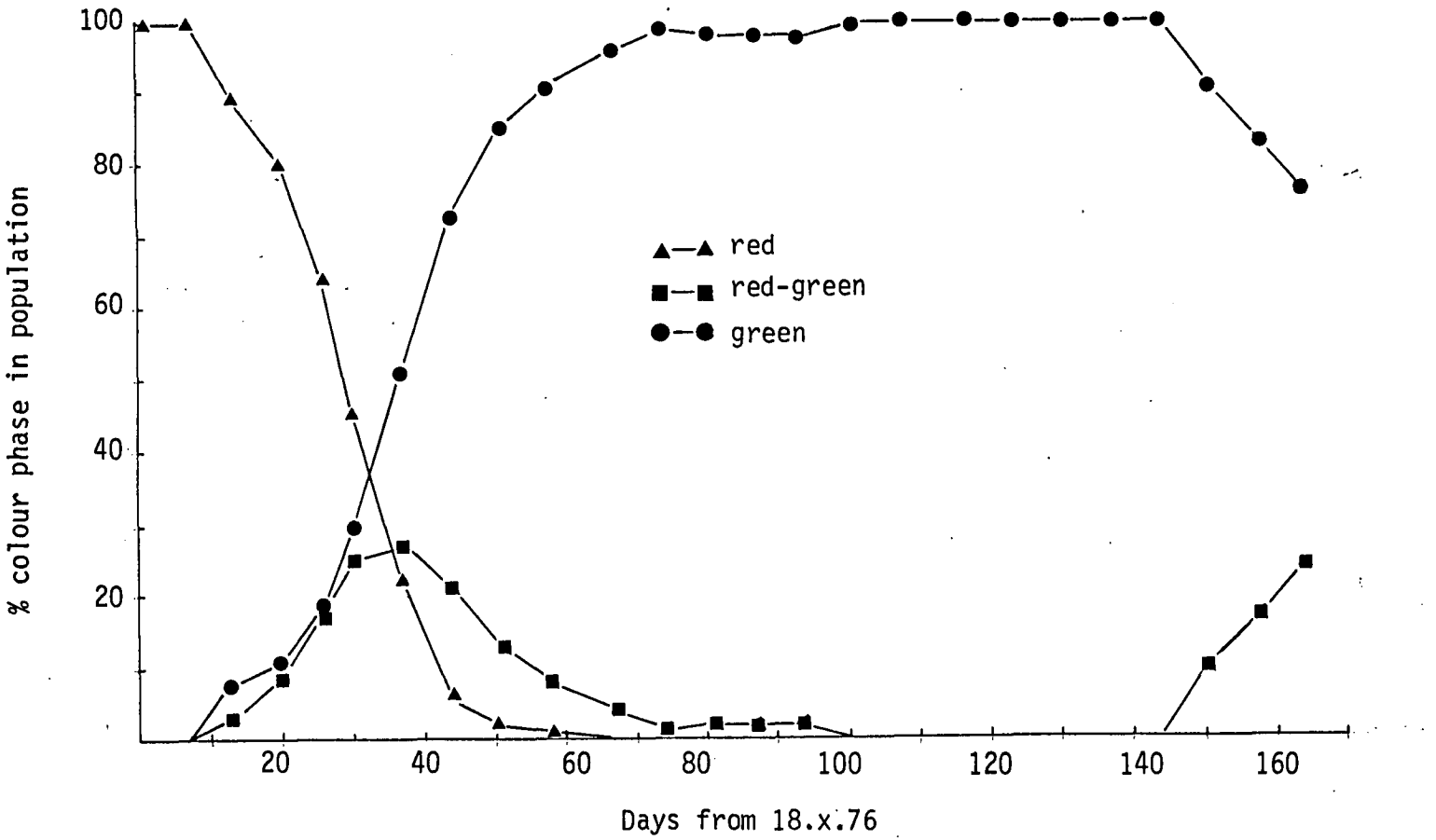


Fig. 243. Percentages (3-point running means) of red, red-green (transitional) and green colour phases in adult *C. bimaculata* population at East Ridgley in 1976/77 season, commencing 18.x.76.

### 2.4.6. Parasitization trials

Larvae were collected at approximately weekly intervals throughout the duration of larval stages in the field at East Ridgley in the 1976/77 and 1977/78 seasons. The larvae were sorted into instars, and in 1976/77 parasitic tachinid eggs present on the larvae were also counted. Larvae were maintained on foliage of *E. regnans* at 24°C and 16 hours photophase and, at the completion of feeding, the prepupae were transferred to gelatin capsules. Records were kept of the fate of individual larvae, and emerging parasitoids collected. Representative specimens were forwarded to the Australian National Insect Collection, C.S.I.R.O., Division of Entomology, Canberra, for identification.

## 2.5. Computations

### 2.5.1. Expression of sampling results

Population sampling data were expressed on a number per shoot basis. Data from East Ridgley in 1975/76 were also expressed in absolute units (numbers per square metre). Data from Bunkers Thinned and Bunkers Grass in 1973/74, where 60 tagged shoots were sampled at regular intervals, were expressed as numbers per shoot (Appendix 8).

Shoot occupancy data for Bunkers Thinned and East Ridgley 1974/75, and for East Ridgley 1975/76, were tabulated from field data sheets, and standard errors calculated (Appendix 9). The data from the sub-samples of occupied shoots were evaluated, and estimates of numbers per shoot were calculated using the relationship:

$$N_{SS} = N_{SS}1 \times \frac{OS}{OS^1} \times \frac{1}{T.S.S.}$$

where $N_{SS}$ = no. of a particular stage per shoot

$N_{SS}1$ = no. of the stage per occupied shoots sub-sample

OS = occupied shoots

$OS^1$ = occupied shoots sub-sample

T.S.S. = total shoots sampled

Date for East Ridgley, 1975/76, were multiplied by the factor 27.36 which was the estimated average number of shoots per square metre throughout the period of sampling (Appendix 10).

2.5.2. Estimation of total populations in each stage

Total populations of each stage were estimated from data obtained using the destructive sampling technique, i.e. for data from Bunkers Thinned, 1974/75, and East Ridgley, 1974/75 and 1975/76.

Approximate total population estimates were obtained by summing the numbers of each stage sampled on successive sampling dates, and multiplying the summed total by the ratio of the mean time between samples to the mean field developmental time of the stage (Table 18). More precise estimates were obtained using Southwood and Jepsons' (1962) method, described by Southwood (1966). This method involves integration of the areas under population curves, and gives a value approximating to the total population at the median age of the stage. Since both egg predation and parasitization could be accounted for, it was possible to gain an accurate estimate of recruitment to the egg stage using this method. However, estimates of recruitment to the larval stages were underestimated, since it was not possible to account for larval "disappearance" which included both predation and active and passive immigration.

Table 18. Total population estimates: (a) using rough method; (b) using Southwood and Jepsons' (1962) method of integrating areas under curves. Populations expressed as numbers per shoot.

| | Bunkers Thinned 1974/75 | | East Ridgley 1974/75 | | East Ridgley 1975/76 | |
|---|---|---|---|---|---|---|
| | (a) | (b) | (a) | (b) | (a) | (b) |
| Eggs | 26.4 | 25.4 | 16.0 | 15.4 | 28.1 | 27.0 |
| L1 | 5.0 | 4.9 | 2.1 | 2.0 | 7.3 | 7.4 |
| L2 | 7.1 | 6.4 | 2.1 | 2.1 | 7.3 | 7.6 |
| L1-2 | 6.2 | 5.4 | 2.0 | 2.1 | 7.3 | 7.5 |
| L3 | 3.4 | 3.6 | 1.7 | 1.6 | 3.0 | 3.2 |
| L4 | 0.9 | 1.0 | 0.6 | 0.5 | 1.3 | 1.2 |

Estimates of larval populations were therefore more correctly "median age" estimates.

Areas under population curves of numbers plotted against time, in days, were estimated by joining successive points by straight lines and resolving resulting areas into a series of triangles and rectangles. The resulting areas were summed to give an estimate of total "stage-days" for each stage. The mean developmental time for each stage (Table 19) was estimated by calculating the mean temperature at the site for the duration of the stage, and finding the corresponding developmental period at the equivalent constant temperature (Section V.2.4.3.). Since development approximates an exponential function of temperature, squared mean temperatures were used to emphasize the importance of maximum temperatures in determining developmental rates. Daily squared mean temperatures were calculated from daily maxima and minima recorded at or near each site (Appendix 11) by the formula:

$$\bar{x}_2 = \sqrt{\frac{a^2 + b^2}{2}}$$

where $\bar{x}_2$ is the daily squared mean temperature

a is the daily maximum temperature

b is the daily minimum temperature

Similarly, squared mean temperatures for the duration of each stage at each site were calculated from daily squared mean temperatures, to emphasize the importance of warmer days in determining developmental rates.

Estimates of total numbers in each stage were derived by dividing the total "stage-days" (the area under the curve of each

Table 19. Mean time between samples, squared mean temperature for duration of stage and mean developmental time of stage at Bunkers Thinned 1974/75 and East Ridgley 1974/75 and 1975/76

| | Mean time between samples | Squared mean temperature | Mean developmental time |
|---|---|---|---|
| B.T. 1974/75 | | | |
| Eggs | 6.3 days | 13.9°C | 9.3 days |
| L1 | 6.1 | 14.2 | 6.7 |
| L2 | 6.3 | 14.4 | 5.1 |
| L1-2 | 6.3 | 14.4 | 11.5 |
| L3 | 6.0 | 14.8 | 5.3 |
| L4 | 6.0 | 15.1 | 6.6 |
| E.R. 1974/75 | | | |
| Eggs | 8.0 | 13.5 | 9.5 |
| L1 | 7.0 | 13.6 | 7.0 |
| L2 | 6.6 | 13.6 | 5.4 |
| L1-2 | 6.5 | 13.6 | 12.4 |
| L3 | 6.2 | 14.3 | 5.6 |
| L4 | 6.3 | 15.2 | 6.5 |
| E.R. 1975/76 | | | |
| Eggs | 5.8 | 15.8 | 8.3 |
| L1 | 5.0 | 15.9 | 5.7 |
| L2 | 4.8 | 15.7 | 4.5 |
| L1-2 | 4.9 | 15.8 | 10.2 |
| L3 | 4.5 | 15.4 | 5.1 |
| L4 | 5.0 | 15.7 | 6.2 |

stage) by the mean developmental time of that particular stage. These estimates (Table 19) were used in the construction of population budgets.

2.5.3. Construction of population budgets

Three partial population budgets were constructed for populations of *C. bimaculata* in three sites, *viz.* Bunkers Thinned, 1974/75; East Ridgley, 1974/75; and East Ridgley, 1975/76. In the first two budgets, populations were expressed as numbers per shoot, but it was possible to express East Ridgley 1975/76 populations in absolute units. Since the East Ridgley 1975/76 population was characterised by high numbers present for a short time (*c.f.* Bunkers Thinned, 1974/75, where the population size was almost identical, but lower numbers were present over a much longer period), it was possible to make reliable counts of adults in both old and new generations. Estimates were also made of pupal mortality in the soil. It was not possible to estimate adult mortality during the overwintering phase, since the location of overwintering sites was often far removed from the study sites.

In the construction of the budgets the rules of Varley *et al.* (1973) were followed. Thus parasitization of larvae was accounted for at the time of attack, rather than at the actual time of death of the larvae due to parasitoid emergence.

2.5.3.1. Eggs

Recruitment to the egg stage was estimated using Southwood and Jepsons' (1962) method of integration. Egg parasitization was estimated by summing the total recorded parasitized eggs in all samples and dividing by total eggs in all samples. Thus a

percentage total egg parasitization was calculated, and an estimate of numbers of parasitized eggs obtained. Egg predation (the only other source of egg mortality) was estimated from eggs unaccounted for, after recruitment to the first larval stage had been subtracted.

2.5.3.2. Larvae

Total populations of first and second instar larvae were estimated independently by integration of areas under population curves (Table 18). First and second instars were treated as a single stage in the budgets due to the similarity of the estimates for first and second instars at East Ridgley in both seasons, and to the higher number of second instars estimated than first instars at Bunkers Thinned. Third and fourth instars were treated as separate stages.

The numbers of braconids and tachinids emerging from sampled fourth instar larvae were summed and percentage levels of parasitization by each parasitoid were obtained. The total population estimates for the first and second instar stage (L1-2), and each succeeding stage were reduced proportionately to account for living larvae parasitized by braconids. In the case of the tachinids, a count was made of all larvae carrying one or more tachinid eggs. It was therefore possible to calculate the total percentage of larvae bearing tachinid eggs in each instar. The relative proportions of new attacks by tachinids in each instar was calculated by assuming that tachinids did not avoid ovipositing on larvae attached during a previous instar. The total percentage of tachinid emergence in the fourth instar was then distributed among the stages on the basis of the relative amount of attack on

each instar. Total population estimates for each succeeding stage were reduced proportionately to account for larvae parasitized in an earlier instar.

Residual mortalities in each stage were estimated by subtraction of all other mortality factors, together with the estimate for the succeeding stage. These residual mortalities were attributed to predation and active and passive emigration.

2.5.3.3. Pupae and adults

Populations of mature and teneral adults were assessed directly at the East Ridgley study site. The maximum number recorded at one sampling date was taken as an estimate of the total population. The percentage of teneral adults emerging in the pupal traps was equated with the numbers of teneral adults recorded in the trees. An estimate of the prepupal population was thereby obtained, from which larval parasitization was subtracted, leaving a nett estimate of the pupal population.

## 3. Results and Observations

### 3.1. Life Cycle

#### 3.1.1. Overwintering sites and dispersal

Overwintering adults (Fig. 244) were rarely encountered during this study. On the "Surrey Hills" plateau (altitude approximately 650 m) (Fig. 233) individual overwintering adults were occasionally located in leaf litter, but none were ever found beneath loose bark at the base of trunks of mature *E. delegatensis*. Numerous overwintering adults were discovered on one occasion (23.viii.1974) in dry areas under loose bark at the base of trunks of mature *E. obliqua* in the Guide River Valley (altitude 340 m). Adults were observed flying in large numbers above mature *E. obliqua* forest in the Inglis River Valley (altitude 150 m) during warm sunny weather on 28.x.1975. These adults were in the red phase (reproductively dormant), and were seen to disperse on to younger *E. obliqua* regeneration higher on the valley slopes.

Large numbers of green-phase (ovigerous) adults (Fig. 245) were observed flying in the Walls of Jerusalem area on the western edge of the Central Plateau on 16.i.1973. These beetles were flying at or above the tree-line (*E. coccifera*) at an altitude of 1200 to 1500 m, and were observed to settle on warm, rocky outcrops in the late afternoon sun. Adults and larvae defoliated *E. delegatensis* regeneration in the adjacent Mersey Valley (altitude 500 m) in the 1972/73 season, and in prior seasons (K.L. Taylor, *pers. comm.*).

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Figs. 244, 245: Phases of adult *Chrysophtharta bimaculata*: (244) red-brown adults in diapause under bark of mature *E. regnans*; (245) green ovigerous adults mating and feeding on young *E. regnans* foliage.

### 3.1.2. Number of generations per season

One generation only of *C. bimaculata* was observed at East Ridgley, 1976/77. Overwintered adults were first observed on the foliage of young *E. regnans* on 18.x.1976, and teneral adults of the new generation were first observed on the foliage on 8.ii.1977. In parental generation females, the first signs of ovary maturation were observed on 5.xi.1976, and ovaries were fully mature by 29.xi.1976, however, significant oviposition did not occur until 20.xii.1976 (Table 20). Ovaries of parental generation females remained mature until March 1977 when beetles of this generation began to disappear from the site. Ovaries of teneral females of the new generation did not mature at this time. In these new generation beetles, fat bodies were laid down, and beetles began to change colour prior to disappearing from the site to overwinter.

Two generations were produced in one season in outside insectaries at Ridgley in the 1976/77 season. Dates of major events are shown in Table 21. Teneral adults of the $F_1$ generation were transferred to a new insectary to produce the $F_2$ generation. The total time elapsed from the first oviposition by the parental generation to the first teneral adult observed in the $F_2$ generation was 148 days, or approximately 21 weeks.

### 3.1.3. Seasonal trends in physiological status of adults

Change in colour phase of adults was observed throughout the 1976/77 season at East Ridgley and this change is shown in Fig. 246. When adults first appeared on foliage at the study site, they were still in the red phase indicative of the diapause condition (Davies 1966). The red coloration changed to the bright green pigmentation of the active, summer phase over a period of approximately one month.

Table 20. Occurrence of events observed in a field population of *C. bimaculata* at East Ridgley during the 1976/77 season.

| Date | Event | Time elapsed |
|---|---|---|
| 18.x.76 | Overwintered adults first observed on foliage in study site | |
| | | 17 days |
| 5.xi.76 | First indication of ovary maturation in $\underset{++}{00}$ | |
| | | 24 days |
| 29.xi.76 | 100% of $\underset{++}{00}$ with fully mature ovaries | |
| | | 21 days |
| 20.xii.76 | First significant oviposition | |
| | | 50 days |
| 8.ii.77 | First teneral adults of $F_1$ generation observed on foliage | |
| | | 71 days |
| 20.iv.77 | Last observation made of $F_1$ adults on foliage in study site | |

Table 21. Occurrence of events in an outside insectary population of *C. bimaculata* at Ridgley during the 1976/77 season.

| Date | Event | Time elapsed |
|---|---|---|
| 27.x.76. | First oviposition | |
| | | 70 days |
| 5.i.77. | First teneral adult of $F_1$ generation | |
| 6-16.i.77 | $F_1$ adults placed in new insectary | 19 days |
| 24.i.77. | First oviposition by $F_1$ | |
| | | 59 days |
| 24.iii.77 | First teneral adult of $F_2$ generation | |
| | | Total = 148 days |

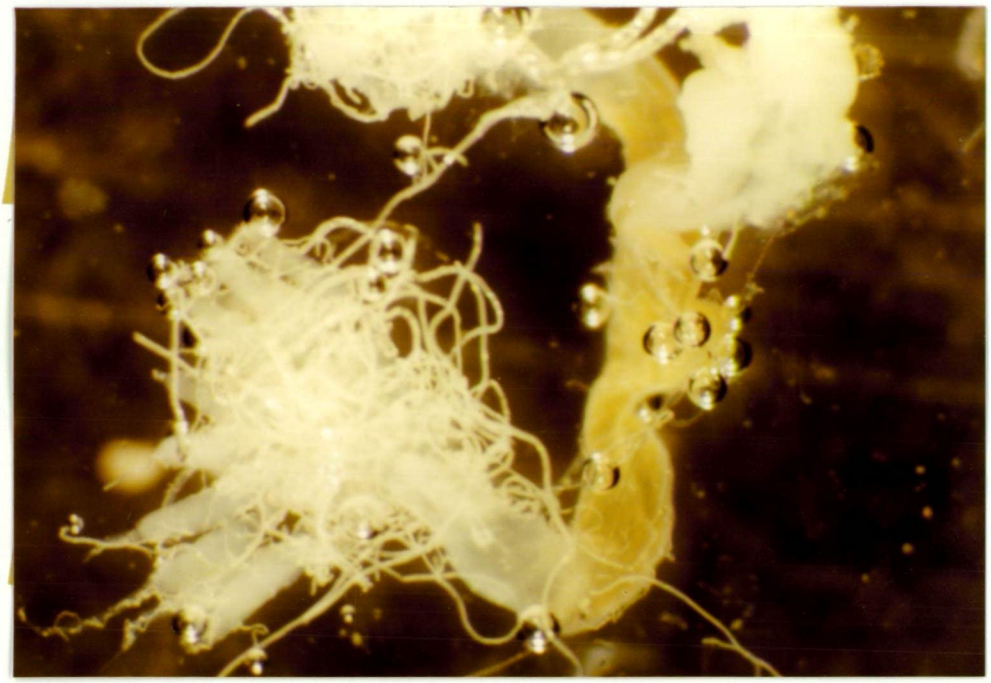
Colour change in males was slightly in advance of in females; partially red individuals of the latter sex being occasionally encountered as late as mid-January. Teneral adults, initially bright green, started to develop red pigmentation late in March. However, no surviving adults of the parental generation were observed developing red pigmentation late in the season in the field. When surviving, field-collected adults of the parental generation were maintained under conditions of natural lighting in the laboratory during autumn,the red coloration was only partially developed.

Ovary maturation (Table 22) commenced well before the colour change from red to green was completed. The development of pinkish red coloration in the calyx region of the ovaries which was visible through the ventral cuticle, was an indication of impending ovary maturation. Similarly, in the males, the development of a bright orange pigmentation of the testes, visible through the ventral cuticle, was an indication of sexual maturity.

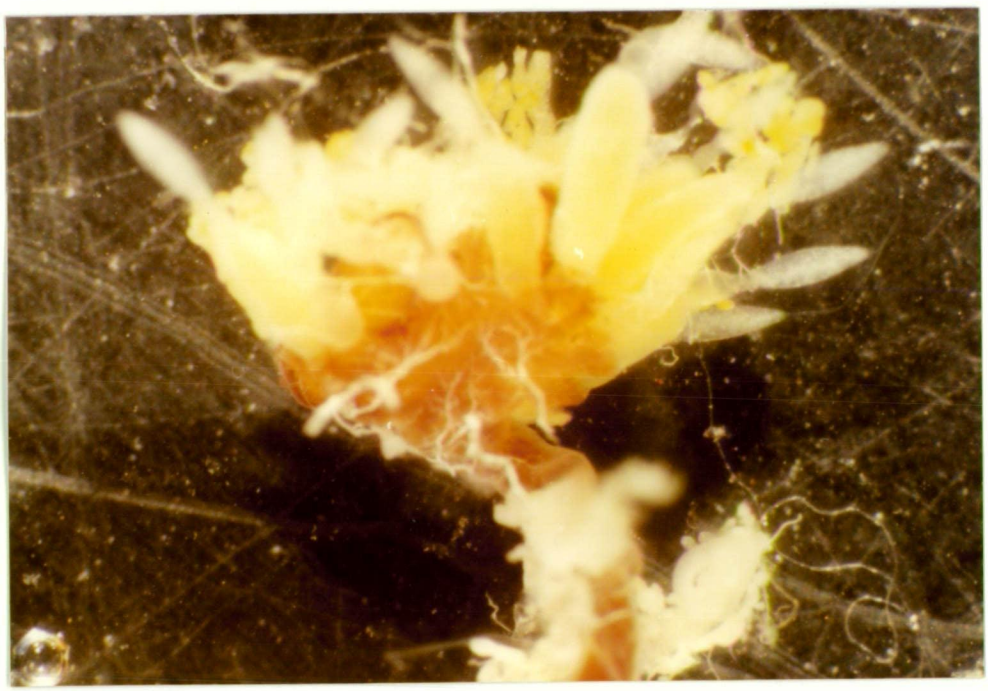
When one-year-old females were induced to diapause for a second winter in the laboratory, the ovaries regressed, but the pinkish red pigmentation of the calyx region remained (Figs. 247, 248). Fifty-six diapausing females, collected under bark in the Florentine Valley, S. Tasmania by H.J. Elliott on 12.viii.1976, were dissected and none was found with regressed ovaries or pinkish red calyx. All had immature ovaries.

### 3.1.4. Phenology

The phenology of *C. bimaculata* was determined during population sampling. The dates of onset of oviposition and commencement of the larval stages varied considerably from season to season (Table 23). When females from East Ridgley



247



248

Figs. 247, 248: Ovarian development in *Chrysophtharta bimaculata* (247) undeveloped ovaries of female in diapause; (248) regressed ovary of post-reproductive female in second diapause. Note red coloration of calyx region.

Table 22. Ovarian condition* of field collected *C. bimaculata* females early in the 1976/77 season at East Ridgley.

| Date | ♀♀ dissected | % C.N.R. | % C.R. | % 0 | % + | % ++ | % +++ |
|---|---|---|---|---|---|---|---|
| 18.x.76 | 3 | 100 | | 100 | | | |
| 5.xi.76 | 8 | 25 | 75 | 25 | 25 | 37.5 | 12.5 |
| 12.xi.76 | 8 | 25 | 75 | 25 | 37.5 | | 37.5 |
| 18.xi.76 | 25 | 4 | 96 | 4 | | 32 | 64 |
| 22.xi.76 | 25 | | 100 | | 8 | 8 | 84 |
| 29.xi.76 | 10 | | 100 | | | | 100 |

*% C.N.R. : Percentage with calyx not red

% C.R. : Percentage with calyx red

% 0 : Percentage with ovaries undeveloped†

% + : Percentage with ovaries partially developed†

% ++ : Percentage with ovaries well developed†

% +++ : Percentage with ovaries fully developed†

†Refer classification (after Davies (1966)), Section V.2.4.4.

Table 23. Dates on which immature stages of *C. bimaculata* were first encountered at field study sites (Bunkers Thinned 1973/74, 1974/75; East Ridgley 1974/75, 1975/76).

| First date of field encounter of: | Bunkers Thinned | | East Ridgley | |
|---|---|---|---|---|
| | 1973/74 | 1974/75 | 1974/75 | 1975/76 |
| Eggs (mass oviposition) | 15.xi.73 | 20.xii.74 | 22.xii.74 | 21.xi.75 |
| L1 | 4.xii.73 | 3.i.75 | | 1.xii.75 |
| L2 | 10.xii.73 | 11.i.75 | 10.i.75 | 8.xii.75 |
| L3 | | 24.i.75 | 17.i.75 | 12.xii.75 |
| L4 | 19.xii.73 | 29.i.75 | 22.i.75 | 18.xii.75 |

were dissected at regular intervals throughout the 1976/77 season, ovary maturation was observed to occur up to one month prior to the onset of major oviposition.

Maximum ovipositional activity coincided with the occurrence of exceptionally warm days in late spring or early summer (Fig. 249) after shoots on host trees were fully expanded. At East Ridgley in 1974/75, oviposition was initiated on 21.xii.74 when the maximum temperature was 25°C. At Bunkers Thinned, in the same season, no exceptionally warm days occurred early in the season, and oviposition occurred far more gradually. However, an exceptionally warm period early in February, with a maximum temperature of 32°C on 7.ii.75, resulted in a second peak of oviposition.

The invasion of the East Ridgley site, by adult *C. bimaculata*, and subsequent oviposition by the females, was observed at first hand in the 1975/76 season. Large numbers of beetles were observed flying down-wind in a warm westerly breeze from the crowns of mature *E. obliqua* at 1600 hours on 21.xi.1975. These beetles by-passed a young plantation of *E. globulus* in their flight path, and alighted on the *E. regnans* plantation block which constituted the study site (Figs. 250, 251) and an adjacent block of *E. delegatensis*. On alighting, the beetles commenced feeding, and mating and oviposition took place. The temperature reached a maximum of 25°C at 1800 hours (Fig. 252). The temperature did not rise above 15°C in the following five days (Fig. 253), but adults remained on the *E. regnans* foliage. No other major movements of beetles were observed in the area, either before or after 21.xi.1975.

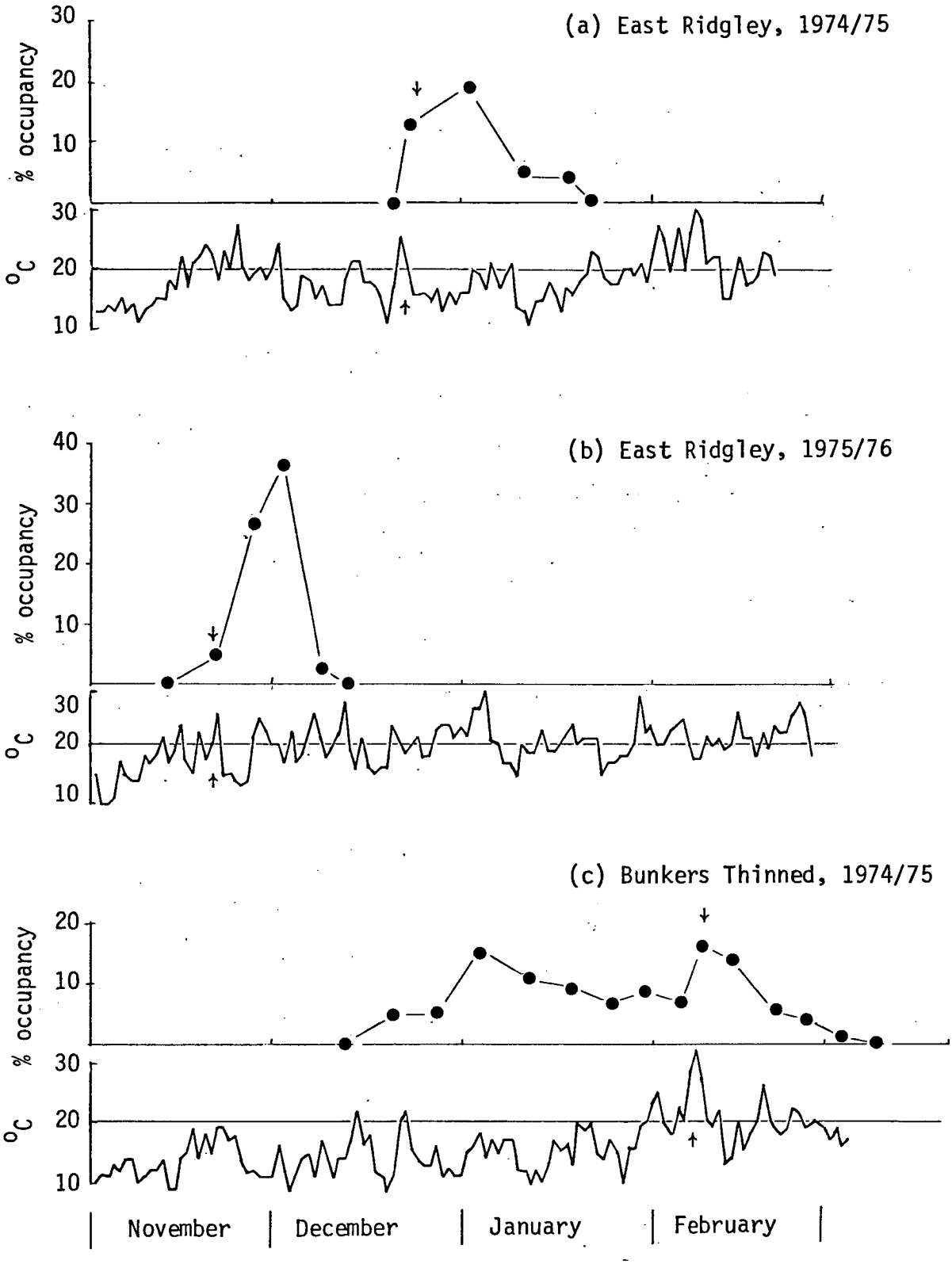



Fig. 249. Percentages of shoots occupied by eggs throughout season with maximum daily temperatures plotted about 20°C.

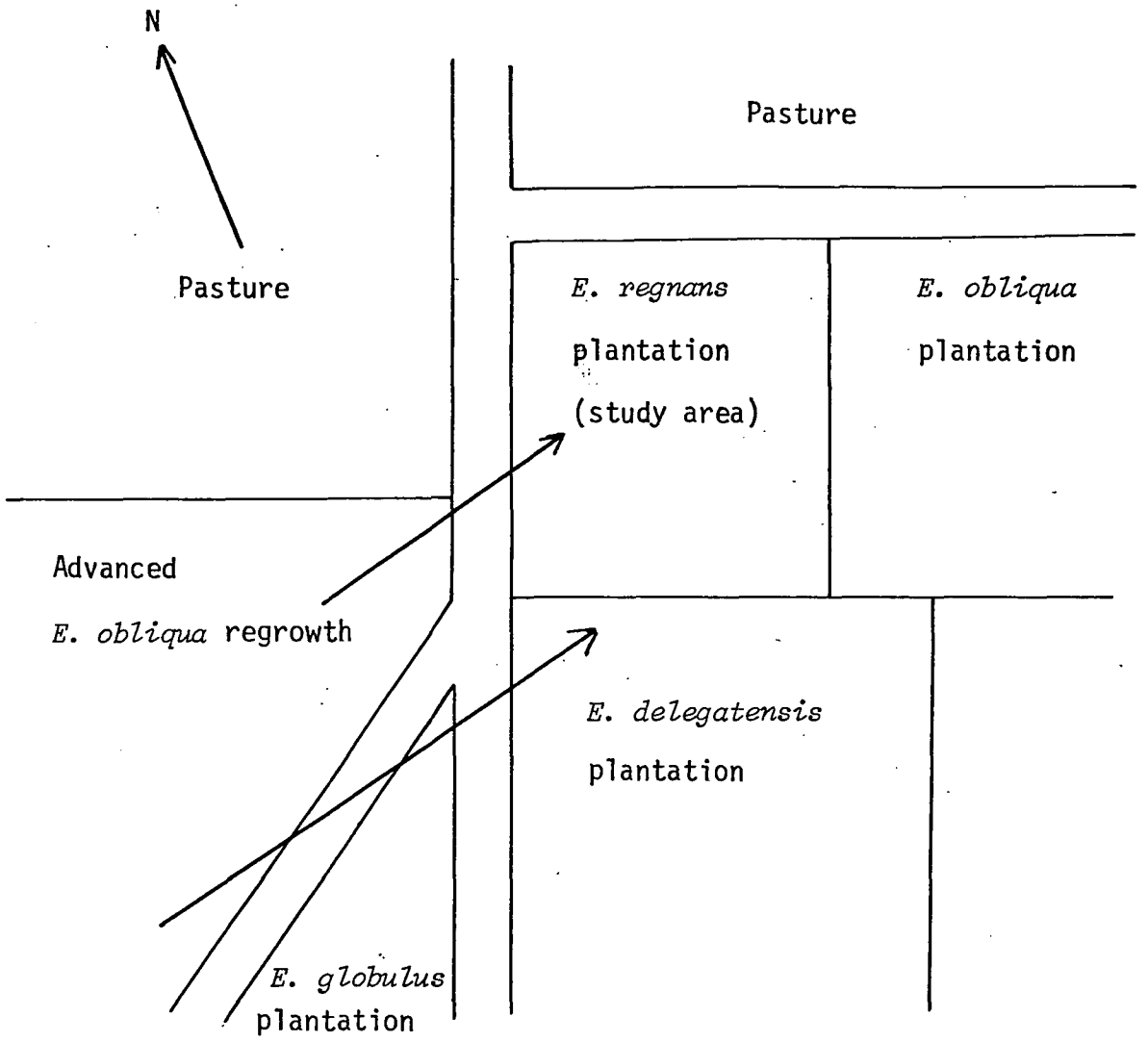



Fig. 250. Map of compartments at East Ridgley study site showing direction of dispersal of *C. bimaculata* from advanced *E. obliqua* regrowth on 21.xi.1975.

Fig. 251: Advanced *E. obliqua* regeneration at East Ridgley study site from which *Chrysophtharta bimaculata* adults migrated on 21.xi.75 to *E. regnans* plantation at extreme left.

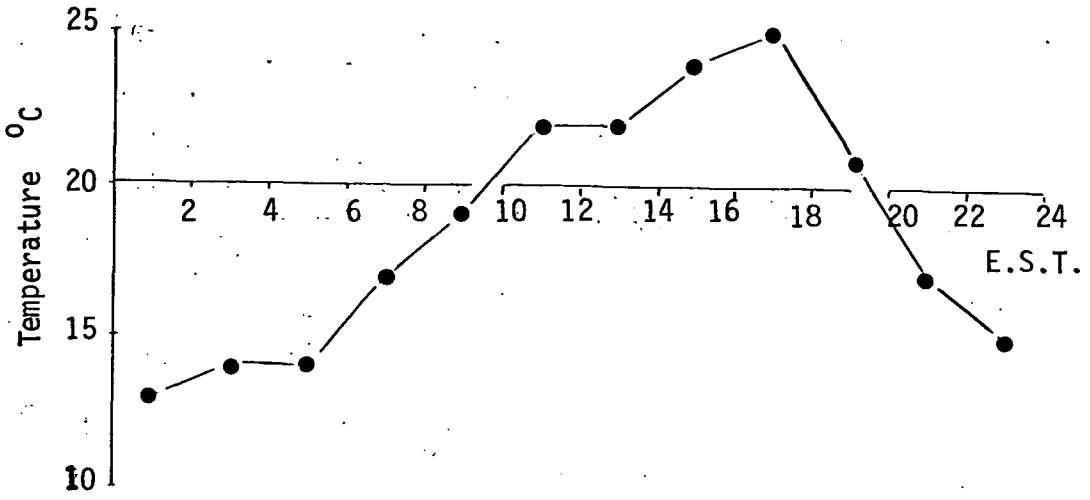



Fig. 252. Two-hourly temperatures at East Ridgley on 21.xi.75 (Eastern Standard Time).

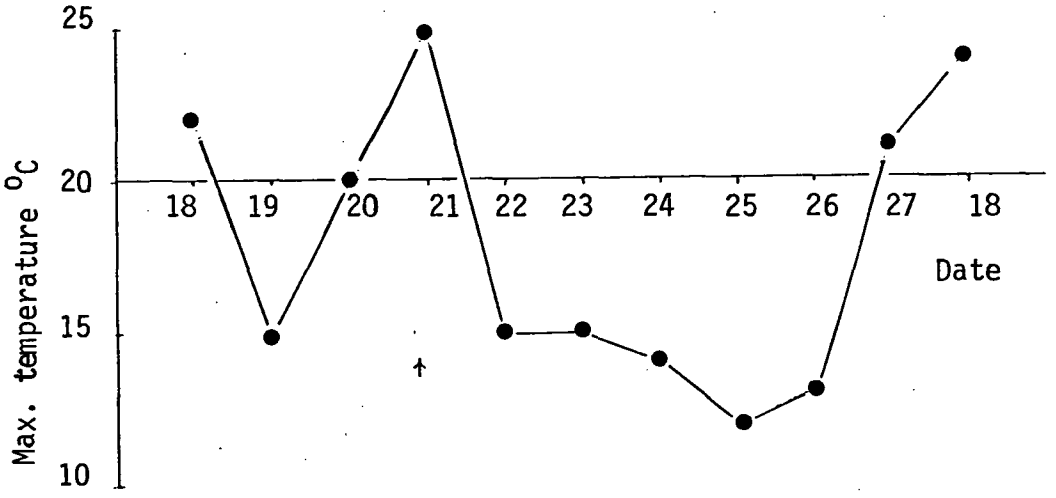



Fig. 253. Maximum daily temperatures at East Ridgley from 18.xi.75 to 28.ix.76 inclusive. Arrow marks congregation of adults and commencement of oviposition (21.xi.75).

## 3.2. Reproductive capacity and behaviour

### 3.2.1. Sex ratio

The percentage of females in a total of 1269 beetles collected by sweeping foliage at East Ridgley in the 1976/77 season was 47.3. In the parental generation (854 beetles), the percentage of females was 47.5, and in the new generation, the percentage was 46.8. The sex ratio was 0.88:1 female to male, and no seasonal change in ratio was observed.

### 3.2.2. Fecundity

The mean number of eggs deposited per female in the laboratory at 23$^{o}$C and 16 hours photophase was 674.62±126.82 (Table 24). The fecundity of females under these conditions varied considerably, ranging from 224 eggs to 1706 eggs. Two females failed to oviposit and were excluded from the trial leaving a total of thirteen females ranging in body weight from 46 mg to 118 mg. Females survived in the laboratory for from 28 days to 139 days. Total fecundity and longevity were unrelated to body size. It was not possible to estimate mean egg batch size, since females oviposited erratically under laboratory conditions.

Progressive oviposition of the two most fecund females is shown in Fig. 254. Rate of oviposition was seen to steadily decrease after the first 80 to 90 days.

### 3.2.3. Distribution of eggs

Trees varied in their attractiveness to *C. bimaculata* females for oviposition. At Bunkers Thinned and Bunkers Grass, in the 1973/74 season, the total number of egg batches deposited on each tagged shoot on each of the ten sample trees at each site were recorded during the initial oviposition peak (Appendix 12). At Bunkers Thinned, the

Table 24. Duration of oviposition and fecundity of three size classes (large, medium and small) of *C. bimaculata* females maintained at 23°C, 16 hours photophase.

| Class | Mass of ♀ (mg) | Duration of oviposition (days) | No. of eggs deposited | Mean eggs per day | Mean eggs per day per mg body mass ($x10^{-2}$) |
|---|---|---|---|---|---|
| Large (100-120mg) | 103 | 28 | 224 | 8.0 | 7.8 |
| | 118 | 123 | 418 | 3.4 | 2.9 |
| | 106 | 118 | 731 | 6.2 | 5.3 |
| | 100 | 100 | 853 | 8.5 | 8.5 |
| | 108 | No oviposition | | | |
| Mean | 106.75±3.94 | 92.25±21.98 | 556.5± 143.79 | 6.53±1.15 | 6.13±1.28 |
| Medium (70-90mg) | 90 | 104 | 570 | 5.5 | 6.1 |
| | 85 | 139 | 1706 | 12.3 | 14.5 |
| | 70 | 96 | 973 | 10.1 | 14.4 |
| | 74 | 41 | 308 | 7.5 | 10.1 |
| | 80 | 123 | 1391 | 11.3 | 14.1 |
| Mean | 79.80±3.61 | 100.60±16.68 | 989.60± 256.44 | 9.34±1.25 | 11.84±1.65 |
| Small (40-60mg) | 48 | No oviposition | | | |
| | 60 | 139 | 382 | 2.8 | 4.7 |
| | 55 | 85 | 289 | 3.4 | 6.2 |
| | 50 | 37 | 276 | 7.5 | 15.0 |
| | 46 | 111 | 649 | 5.9 | 12.8 |
| Mean | 52.75±3.04 | 93.00±21.68 | 399.00± 66.61 | 4.90±1.10 | 9.68±2.50 |

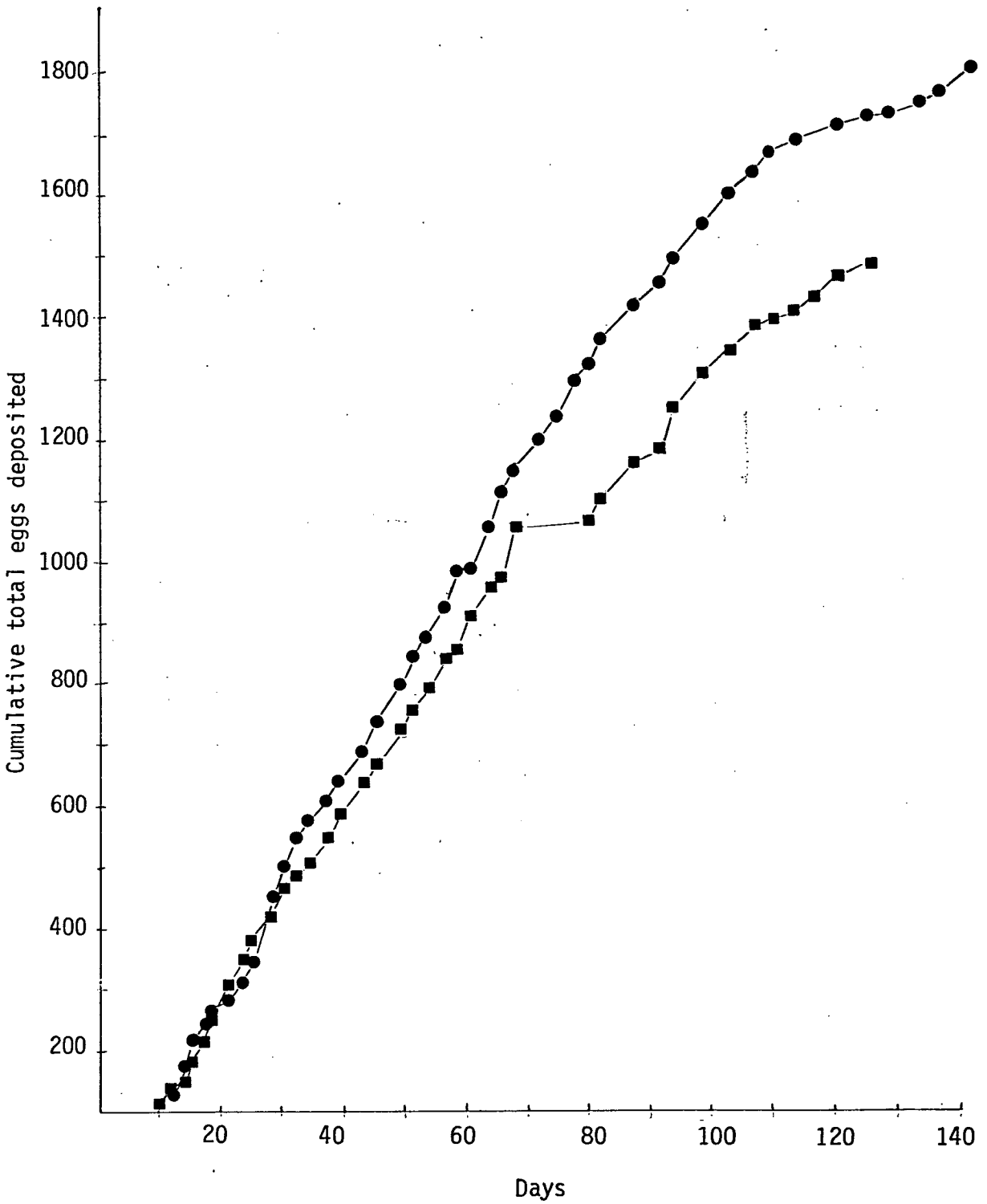



Fig. 254. Cumulative total eggs deposited by two female *C. bimaculata* held at 23°C, 16 hours photophase.

Table 25. Total egg batches recorded on individual trees at Bunkers Thinned and Bunkers Grass study sites, 1973/74 season (six tagged shoots per tree).

| Tree | Bunkers Thinned | | Bunkers Grass | |
|---|---|---|---|---|
| | (a) | (b) | (a) | (b) |
| T1 | 9 | 1.5 | 2 | 0.3 |
| T2 | 4 | 0.7 | 17 | 2.8 |
| T3 | 13 | 2.2 | 23 | 3.8 |
| T4 | 13 | 2.2 | 8 | 1.3 |
| T5 | 6 | 1.0 | 2 | 0.3 |
| T6 | 3 | 0.5 | 8 | 1.3 |
| T7 | 6 | 1.0 | 9 | 1.5 |
| T8 | 8 | 1.3 | 9 | 1.5 |
| T9 | 4 | 0.7 | 27 | 4.5 |
| T10 | 3 | 0.5 | 8 | 1.3 |
| Mean | 1.16±0.20 | | 1.76±0.47 | |

(a) : Total batches deposited on tagged shoots

(b) : Total batches per shoot

mean number of batches per shoot on a sample tree varied from 0.50 to 2.17, and at Bunkers Grass, from 0.33 to 4.50 (Table 25).

Within trees, egg batch distribution among shoots at both sites during peak oviposition closely approximated a negative binomial distribution (Table 26).

### 3.3. Weather induced stress

An attempt was made to relate change in *C. bimaculata* populations to White's Stress Index (White 1969). *C. bimaculata* populations were in outbreak proportions in N.W. Tasmania during the period 1971 to 1973. However, during this time the Stress Index was highly negative (Fig. 255), indicating that trees were undergoing minimal moisture stress. In the 1973/74 and 1974/75 seasons the stress index rose steeply, but this period corresponded with a rapid decline in *C. bimaculata* populations, which have generally remained at low levels to the present time, despite changes in the index.

The period of decline of *C. bimaculata* populations corresponded, however, with a period when winter rainfalls were much greater than average (1974 to 1976) (Fig. 256).

### 3.4. Natural enemies

#### 3.4.1. Predators

A number of insect predators were observed to feed on eggs and larvae of *C. bimaculata* at both the Ridgley and Surrey Hills study sites. The major species was the coccinellid *Cleobora mellyi* Mulsant (Coccinellinae:Psylloborini) (Fig. 257). A second coccinellid, *Harmonia conformis* (Boisduval) (Coccinellinae:Coccinellini) was less abundant. The cantharid beetle, *Chauliognathus pulchellus* Macleay,

Table 26. Dispersion of egg batches of *C. bimaculata* among shoots at Bunkers Thinned and Bunkers Grass study sites, 1973/74 season (60 tagged shoots per site).

| Site and Date | | No. egg batches per shoot 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | $x^2$* | K | Mean |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Bunkers Thinned | | | | | | | | | | | | | |
| 4.xii.73 | Obs | 34 | 18 | 5 | 3 | | | | | | | | |
| | Exp | 33.8 | 18.0 | 6.0 | 1.6 | | | | | | 0.022 2 d.f. | 3.882 | 0.617 |
| 7.xii.73 | Obs | 32 | 20 | 3 | 5 | | | | | | | | |
| | Exp | 32.9 | 18.2 | 6.7 | 2.0 | | | | | | 0.259 2 d.f. | 3.260 | 0.683 |
| 10.xii.73 | Obs | 33 | 16 | 6 | 5 | | | | | | | | |
| | Exp | 32.3 | 17.3 | 6.8 | 2.4 | | | | | | 0.465 2 d.f. | 2.120 | 0.717 |
| Bunkers Grass | | | | | | | | | | | | | |
| 12.xii.73 | Obs | 24 | 18 | 7 | 4 | 3 | 2 | 0 | 1 | 1 | | | |
| | Exp | 24.8 | 15.1 | 8.8 | 5.0 | 2.8 | 1.6 | 0.9 | 0.5 | 0.3 | 1.284 4 d.f. | 1.105 | 1.350 |
| 14.xii.73 | Obs | 21 | 15 | 10 | 7 | 0 | 3 | 1 | 2 | 1 | | | |
| | Exp | 21.2 | 14.8 | 9.4 | 5.8 | 3.5 | 2.1 | 1.3 | 0.8 | 0.4 | 0.441 4 d.f. | 1.216 | 1.650 |

*Classes where expected frequencies less than 5 combined.

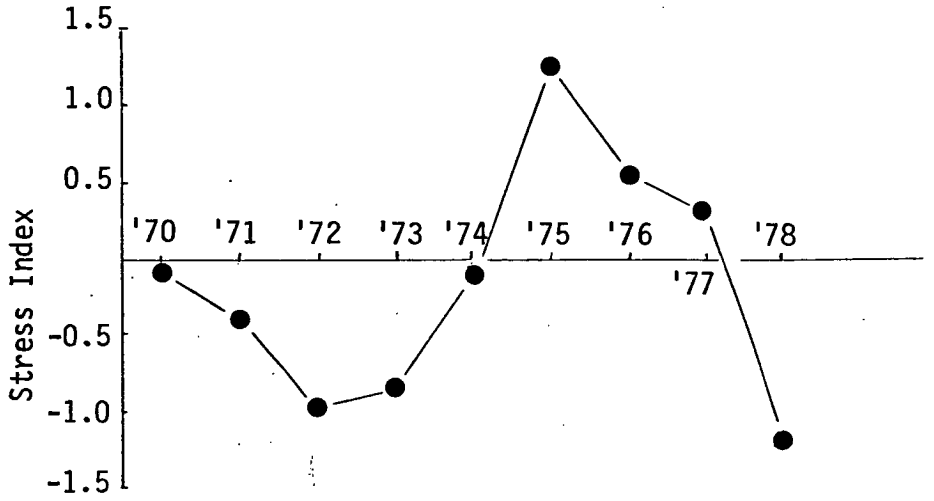



Fig. 255

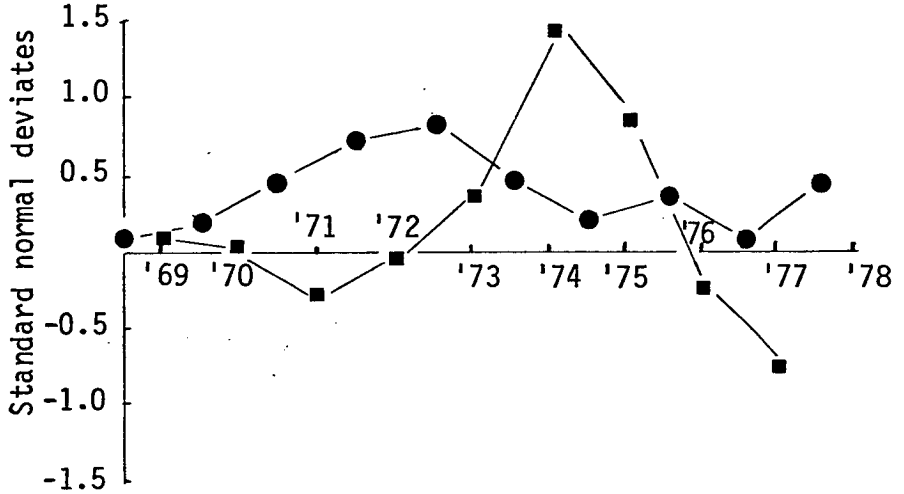



Fig. 256

Fig. 255. Stress index (White 1969) for Burnie, Tasmania from 1970 to 1978 inclusive (3-year running means).

Fig. 256. Summer rainfall ( ●-● ) and winter rainfall ( ■-■ ) for Burnie, Tasmania from 1969 to 1978 inclusive, plotted as standard normal deviates about mean (3-year running means). Mean rainfall taken over period 1887 to 1978.

was often present contemporaneously with *C. bimaculata* eggs, and was observed to feed on them. The pentatomid bug, *Cermatulus nasalis* (Westwood) attacked larvae and, on one occasion, was observed feeding on an adult beetle. Reduviid and mirid bugs were also occasionally observed feeding on eggs and larvae.

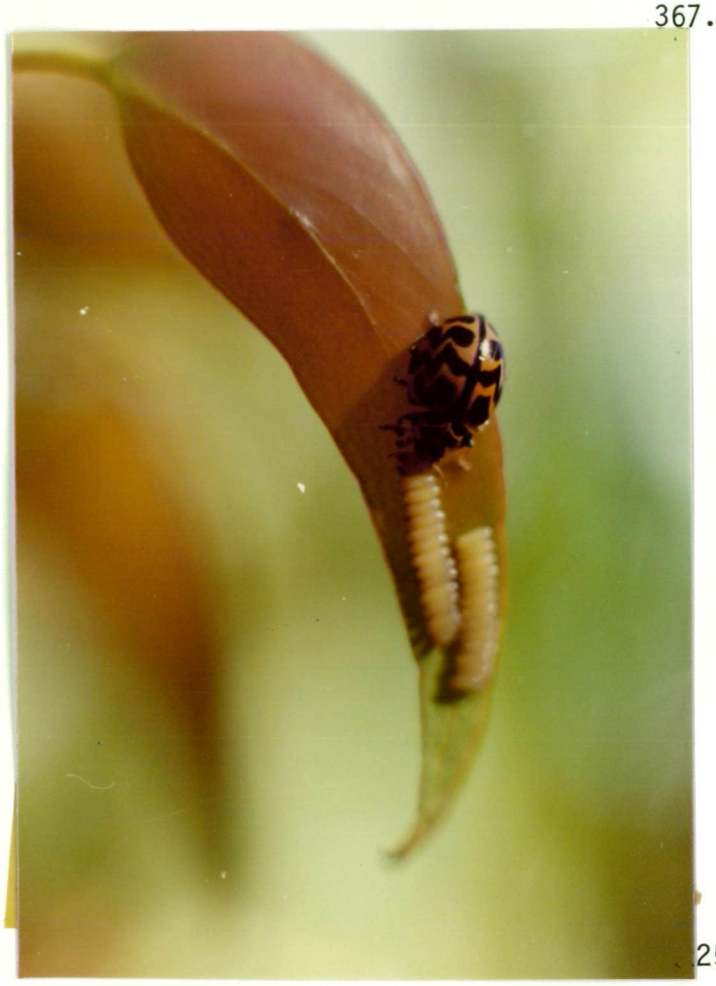
Adult *C. bimaculata* were attacked by the black currawong (*Strepera fuliginosa* Gould) which was a common bird in the Surrey Hills area. The finding of chitinous fragments of *C. bimaculata* adults (identifiable from the black marks on the pronotum) in crop regurgitates was evidence of this predatory activity.

3.4.1.1. Field observations

The two coccinellid species, *Cl. mellyi* and *H. conformis* overwintered as adults in large mixed aggregations under bark and in hollow trees. They were sometimes found in association with overwintering *C. bimaculata* adults or other paropsid species under bark.

Adult coccinellids of both species occurred on foliage in spring at the time of mass oviposition by *C. bimaculata*. Coccinellid egg batches were rarely encountered, but highly active first instar larvae fed on late egg batches of *C. bimaculata*. *Cl. mellyi* larvae preyed on larvae of *C. bimaculata* up to their own body size (Fig. 258). The defensive secretion of large *C. bimaculata* larvae paralysed and sometimes killed small *Cl. mellyi* larvae. Both coccinellid species fed on alternative foods, especially the psyllid *Glycaspis* sp. which was often present in the study areas.

In the course of *C. bimaculata* population sampling at the East Ridgley study site in the 1975/76 season, the occurrence of



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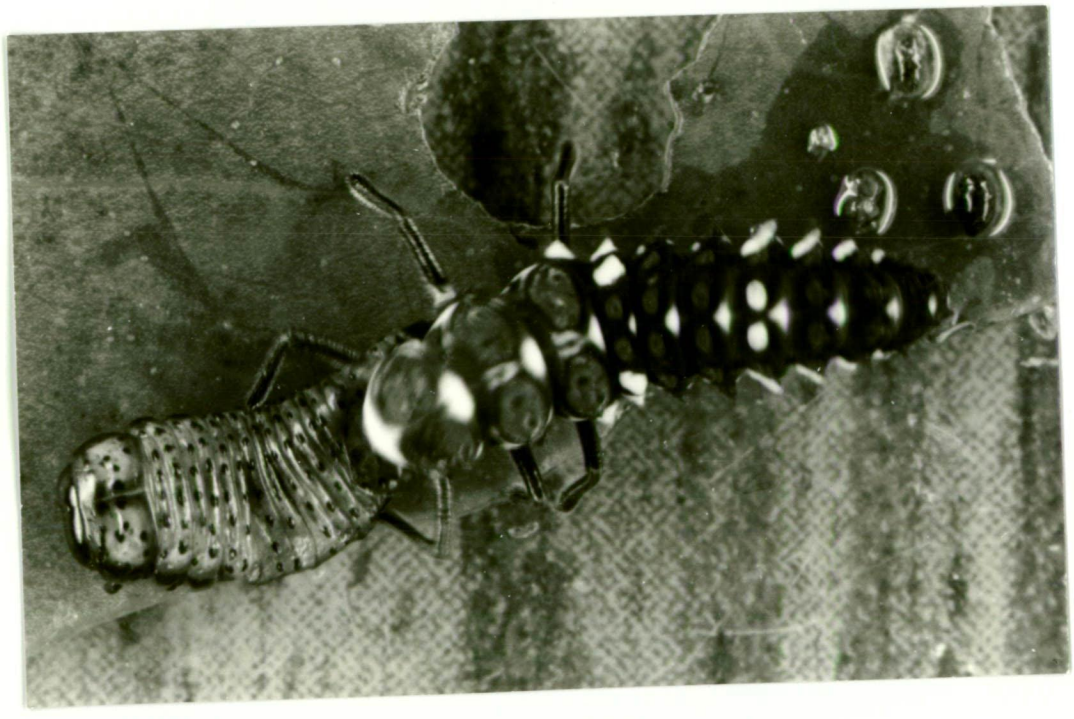

258

Figs. 257, 258: Coccinellid predator *Cleobora mellyi* Mulsant (257) adult consuming egg batch of *Chrysophtharta bimaculata*, (258) larva consuming larva of *Chrysophtharta bimaculata*.

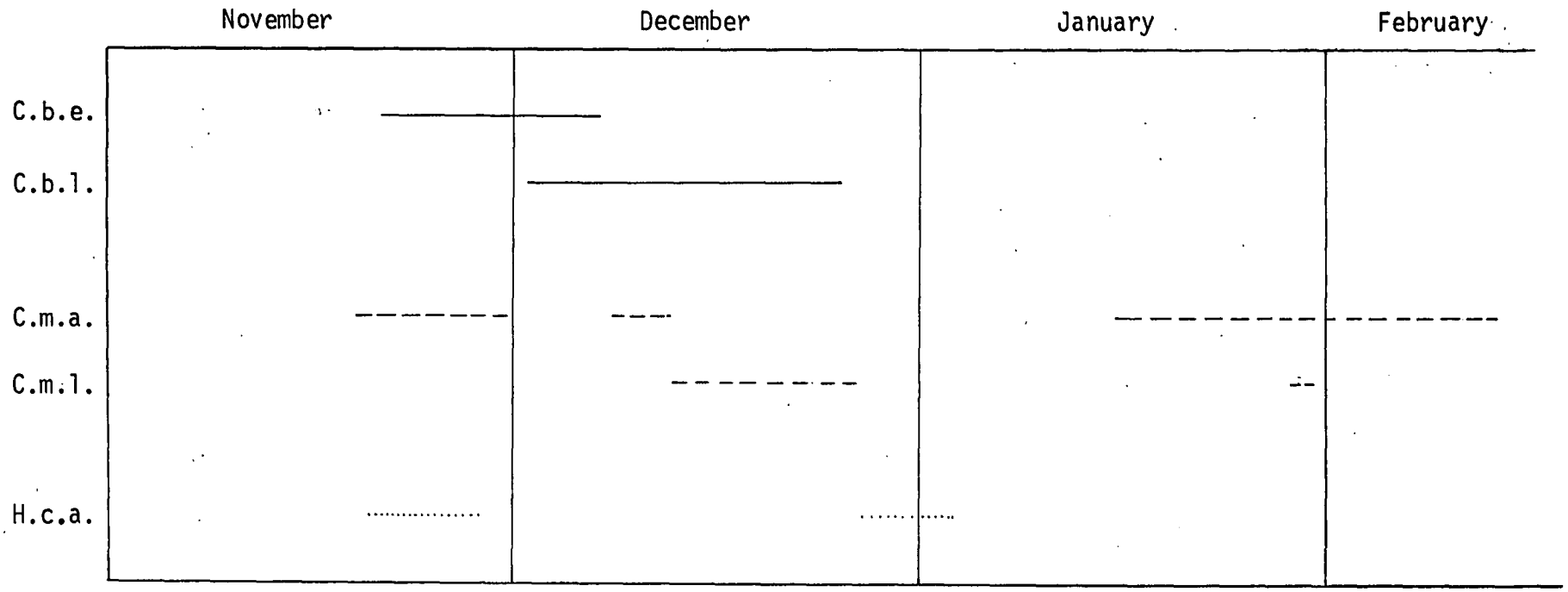


Fig. 259. Occurrences of *C. bimaculata* eggs (C.b.e.), *C. bimaculata* larvae (C.b.l.), *Cleobora mellyi* adults (C.m.a.), *Cl. mellyi* larvae (C.m.l.), and *Harmonia conformis* adults (H.c.a.) on shoots at East Ridgley study site, November 1975 to February 1976.

*Cl. mellyi* and *H. conformis* on sampled shoots was also recorded (Fig. 259). Most occurrences of adult coccinellids were recorded while *C. bimaculata* eggs were present, but *Cl. mellyi* larvae did not appear on shoots until after *C. bimaculata* eggs had hatched. No *H. conformis* larvae were recorded.

3.4.1.2. Laboratory feeding trials with *Cl. mellyi*

When eight pairs of field collected, mature adults of *Cl. mellyi* were maintained on *C. bimaculata* eggs for eight days, the mean number of eggs consumed per adult per day under laboratory conditions was 19.8±1.8 eggs (Table 27). Field collected adults failed to survive in the laboratory on a diet consisting entirely of first and second instar *C. bimaculata* larvae. Larvae completed their development on a diet consisting entirely of *C. bimaculata* eggs, and on a mixed diet of eggs and larvae, but did not survive on a diet consisting entirely of larvae.

3.4.2. Parasitoids

Hymenopterous and dipterous parasitoids were reared from *C. bimaculata* eggs and larvae collected from the Ridgley and Surrey Hills study sites.

3.4.2.1. Egg parasitoids

*Enoggerella nassaui* Girault (Pteromalinae) was reared from eggs collected at Surrey Hills study sites. An unidentified species of the sub-family Inostemmatinae (Platygasteridae) was reared from eggs collected at the East Ridgley study area. Parasitised eggs were recognised by their failure to hatch in the normal incubation period, and by the subsequent development of black pigmentation at one end (Fig. 260).

Table 27. Daily consumption of *C. bimaculata* eggs by *Cleobora mellyi* in the laboratory at 23°C, 16 hours photophase.

| No. of adults | Feeding period | Total eggs eaten per pair (range) | Mean eggs eaten per adult per day (± S.E.) |
|---|---|---|---|
| 16 (8 pairs) | 13 | 515.5 (291-643) | 19.8±1.8 |

260

261

Figs. 260, 261: Parasitoids of *Chrysophtharta bimaculata* (260) parasitized egg batch, (261) tachinid parasitoids (middle and left) and ichneumonid hyperparasitoid (*Mesochorus* sp.) of tachinids (right).

3.4.2.2. Larval parasitoids

Two dipterous species belonging to the family Tachinidae (Goniinae:Blondeliini) were reared from prepupae, and occasionally pupae of *C. bimaculata* (Fig. 261). They were identified as *Anagonia rufipes* (Macquart) and *Paropsivora* sp. While *A. rufipes* most frequently emerged from field collected fourth instar larvae, *Paropsivora* sp. was more common among larvae collected in the field during their first three instars (Table 28). *Anagonia rufipes* accounted for approximately three-quarters of tachinid emergences.

Parasitization of larvae by tachinids was often indicated by the presence of one or more small white eggs on the larval cuticle. On eclosion, the tachinid maggot entered the host larva, but remained inconspicuous until the prepupal stage of the host. Maggots underwent rapid growth during the host prepupal phase, and either formed a puparium within the host cuticle, or emerged just prior to the puparial stage. Although more than one parasitoid egg was frequently observed on a host larva (Table 29) multiple parasitization did not occur.

Both tachinid species were hyper-parasitized by an hymenopteran, *Mesochorus* sp. (Ichneumonidae:Mesochorinae) (Fig. 261). At East Ridgley in the 1977/78 season, of the 82 successful emergences from tachinid infested field collected first to fourth instar larvae, 12 (15%) were the hyper-parasitoid, *Mesochorus* sp.

One hymenopterous species, *Eadya paropsidis* Huddleston (Braconidae:Euphorinae),was reared from larvae collected at East Ridgley and Surrey Hills. *E. paropsidis* was observed parasitizing first and second instar larvae, but since eggs were deposited subcutaneously, no mark of parasitization remained. Larvae of

Table 28. Percentages of *A. rufipes* and *Paropsivora* sp. emerging in the laboratory from field collected larvae of each instar at East Ridgley, 1977/78. (Total tachinids emerging = 48).

| Larval instar | *A. rufipes* | *Paropsivora* sp. |
|---|---|---|
| L1 | - | 4.2 |
| L2 | 2.1 | 4.2 |
| L3 | 8.3 | 12.4 |
| L4 | 62.5 | 6.3 |
| Total | 72.9 | 27.1 |

Table 29. Frequency of occurrence of tachinid eggs on 1,432 *C. bimaculata* larvae collected at East Ridgley, 1977/78.

| No. eggs | L1 | | L2 | | L3 | | L4 | |
|---|---|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % | No. | % |
| zero eggs | 376 | 96.4 | 253 | 94.5 | 309 | 88.2 | 367 | 86.6 |
| 1 egg | 11 | 2.8 | 11 | 4.1 | 24 | 6.9 | 40 | 9.4 |
| 2 eggs | 2 | 0.5 | 2 | 0.7 | 9 | 2.6 | 9 | 2.1 |
| >2 eggs | 1 | 0.3 | 2 | 0.7 | 8 | 2.3 | 8 | 1.9 |
| Total | 390 | | 268 | | 350 | | 424 | |
| % with one or more eggs | | 3.6 | | 5.5 | | 11.8 | | 13.4 |

*E. paropsidis* remained inconspicuous within the host, until the host entered the prepupal stage. The parasitoid larva then developed rapidly, and split the host cuticle to emerge and spin a white cocoon. Emergence of adult *E. paropsidis* from cocoons was extremely rare in the laboratory.

3.4.2.3. Larval parasitization studies

Detailed studies were made of larval parasitization at the East Ridgley study site in the 1976/77 and 1977/78 seasons. Further information on larval parasitization was gained from general population sampling at this site in the two preceding seasons (1974/75 and 1975/76). Over the four season period the percentage of larvae parasitized by braconids decreased from 64 percent to 21 percent, and the tachinid parasitized larvae increased from 6 percent to 14 percent (Table 30).

The maximum level of braconid parasitization occurred in the second instar (Table 31). In contrast, tachinid parasitization increased to a maximum level in the fourth instar. First instar braconid larvae dissected from hosts were strongly mandibulate which presumably conferred competitive superiority in encounters with tachinid maggots.

Braconid parasitization was heaviest early in the season when the larval population consisted mainly of early instars, but showed a rapid decline by mid-season (Figs. 262, 263). Tachinid parasitization remained low and relatively constant throughout the 1976/77 season (Fig. 262), but in the following season, when braconid parasitization was lower, tachinid parasitization increased to a peak in the latter part of the season (Fig. 263).

Table 30. Fate of field collected L4 *C. bimaculata* over four consecutive seasons at East Ridgley. (Data for 1974/75 and 1975/76 seasons taken from population sampling data for budgets.)

| Fate of larva | 1974/75 | 1975/76 | 1976/77 | 1977/78 |
|---|---|---|---|---|
| % Adult *C. bimaculata* emerged | 18.8 | 52.6 | 40.4 | 55.0 |
| % Braconid | 64.2 | 34.6 | 36.6 | 21.5 |
| % Tachinid | 5.7 | 8.5 | 7.6 | 13.7 |
| % Mortality due to unknown cause | 11.3 | 4.3 | 15.4 | 9.8 |

Table 31. Ultimate fate of field collected larvae of each instar maintained in the laboratory until pupation.
(A = % pupating; B = % parasitized by braconid; T = % parasitized by tachinid; X = % dying of unknown cause at prepupal stage.)

| Stage | 1976/77 | | | | 1977/78 | | | |
|---|---|---|---|---|---|---|---|---|
| | A | B | T | X | A | B | T | X |
| L1 | 64.5 | 30.7 | 0.6 | 4.2 | 78.4 | 9.0 | 3.3 | 9.3 |
| L2 | 50.9 | 41.6 | 0.9 | 6.6 | 63.4 | 21.9 | 3.6 | 11.1 |
| L3 | 39.4 | 38.1 | 4.7 | 17.8 | 59.0 | 20.7 | 6.5 | 13.8 |
| L4 | 40.4 | 36.6 | 7.6 | 15.4 | 55.0 | 21.5 | 13.7 | 9.8 |

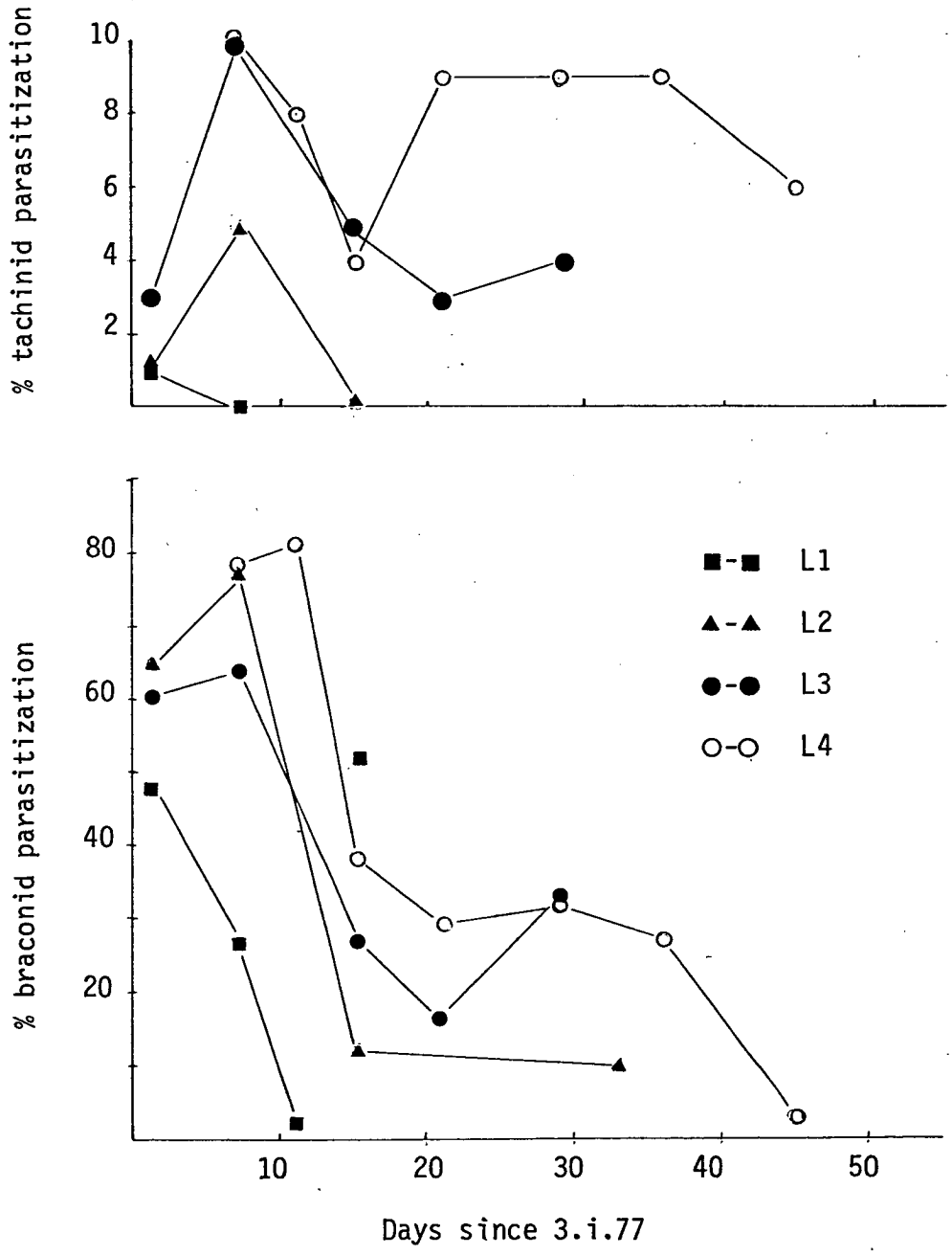


Fig. 262. Percentage parasitization of *C. bimaculata* larvae of different instars collected from East Ridgley, January to February 1977.

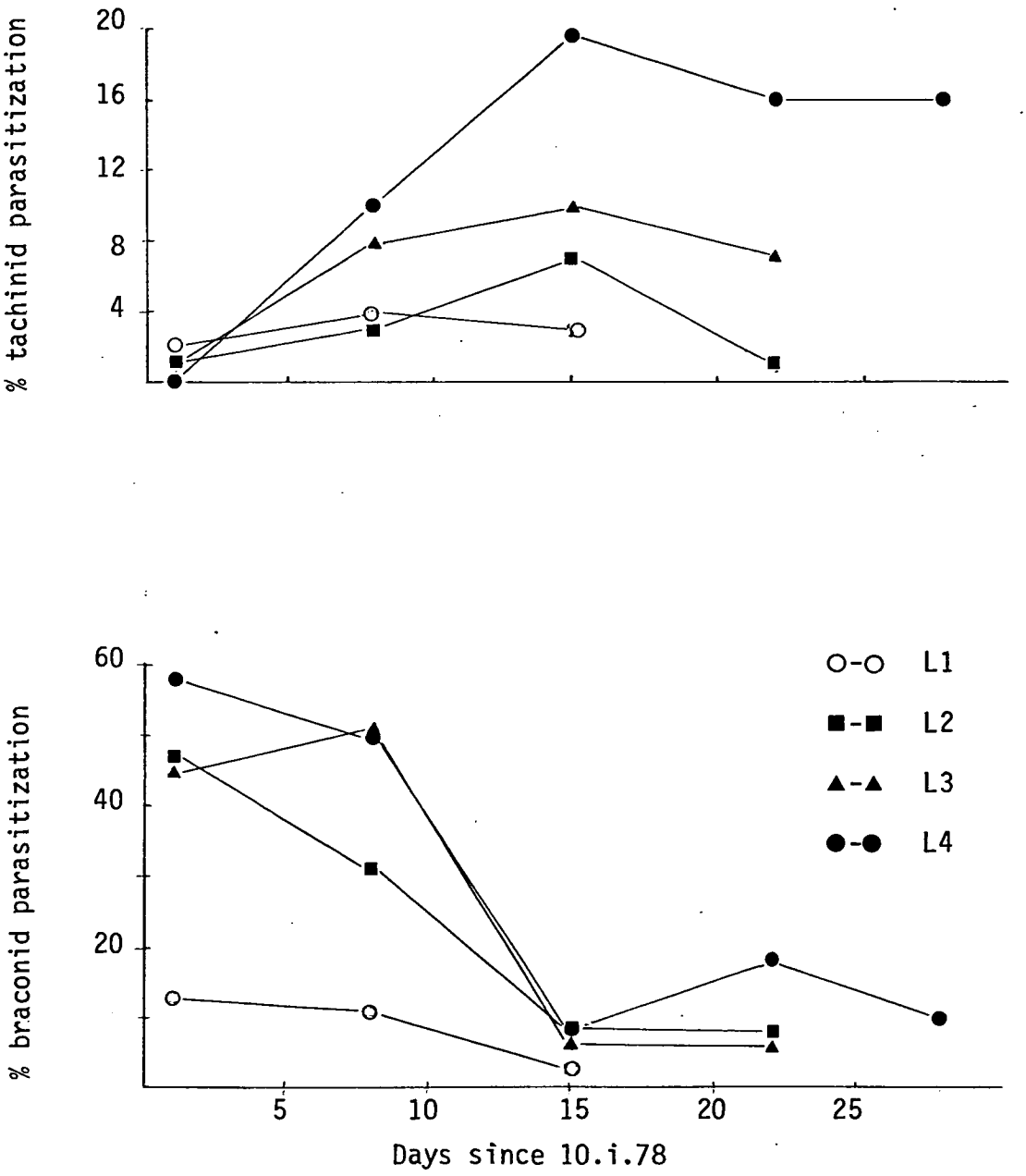


Fig. 263. Percentage parasitization of *C. bimaculata* larvae of different instars collected from East Ridgley, January to February 1978.

### 3.4.3. Pathogens

Dead adults were frequently encountered under bark, apparently having been killed in the overwintering phase by a white entomophagous fungus (Fig. 264). The incidence of cadavers infested by this fungus was greatest in damp areas under bark.

When active, healthy *C. bimaculata* adults were placed on cultures of this fungus, sub-cultured from infested cadavers collected under bark in the Florentine Valley, and incubated at $4^{o}C$ for one week; all beetles became infested by the fungus within four days and died. The fungus was recultured and identified as *Metarhizium* sp.

Field collected adults held in the laboratory occasionally died as the result of infestation by a mermithid nematode. Only one nematode emerged from each host. The occurrence of this pathogen was extremely rare.

### 3.4.4. Population biology

Partial population budgets were prepared for populations of *C. bimaculata* at Bunkers Thinned in the 1974/75 season, and at East Ridgley in the 1974/75 and 1975/76 seasons (Tables 32, 33, 34). Budgets for 1974/75 were expressed on a numbers per shoot basis, while the 1975/76 budget was expressed in absolute units (numbers per square metre). Adult populations and pupal mortality were also estimated in 1975/76.

Predation was a considerably greater mortality factor among eggs than was parasitization, and accounted for 62 to 74 percent of the total oviposition. Parasitization of eggs due to *Enogerrella nassaui* at Bunkers Thinned was higher than that due to the platygasterid parasitoid at East Ridgley.

Fig. 264: Adult *Chrysophtharta bimaculata* killed by fungal pathogen *Metarhizium* sp.

Table 32. Budget for immature stages of *C. bimaculata* evaluated at Bunkers Thinned, "Surrey Hills" 1974/75. Population expressed on numbers per shoot basis.

| Stage | Mortality factors | Survivorship (Nos./shoot) | Mortality (Nos./shoot) | % Mortality |
|---|---|---|---|---|
| Eggs | | 25.4 | | |
| | *Enoggerella nassaui* | | 4.2 | 16.5% |
| | Predation (mainly *Cleobora mellyi*) | | 15.8 | 62.2% |
| Larvae 1-2 | | 5.4 | | |
| | *Eadya paropsidis* | | 0.1 | 2.0 |
| | Tachinids | | 0.8 | 14.3 |
| | Predation / Dispersal | | 1.5 | 27.5 |
| Larvae 3 | | 3.0 | | |
| | Tachinids | | 0.4 | 14.5 |
| | Predation / Dispersal | | 1.9 | 63.6 |
| Larvae 4 | | 0.7 | | |
| | Tachinids | | 0.1 | 10.2 |
| | | 0.6 | | |
| | | | 24.8 | 97.6 |

Table 33. Budget for immature stages of *C. bimaculata* evaluated at East Ridgley, 1974/75. Population expressed on numbers per shoot basis.

| Stage | Mortality factors | Survivorship (Nos./shoot) | Mortality (Nos./shoot) | % Mortality |
|---|---|---|---|---|
| Eggs | | 15.4 | | |
| | Platygasterid | | 1.9 | 12.3 |
| | Predation (mainly *Cleobora mellyi*) | | 11.4 | 74.0 |
| Larvae 1-2 | | 2.1 | | |
| | *Eadya paropsidis* | | 1.3 | 64.2 |
| | Tachinids | | 0.0 | 1.3 |
| | Predation / Dispersal | | 0.2 | 9.5 |
| Larvae 3 | | 0.6 | | |
| | Tachinids | | 0.0 | 1.0 |
| | Predation / Dispersal | | 0.3 | 55.4 |
| Larvae 4 | | 0.3 | | |
| | Tachinids | | 0.0 | 3.4 |
| | | 0.3 | | |
| | | | 15.1 | 98.1 |

Table 34. Budget for *C. bimaculata* evaluated at East Ridgley, 1975/76. Population expressed on numbers per square metre basis.

| Stage | Mortality factors | Survivorship (Nos./sq.m) | Mortality | % Mortality |
|---|---|---|---|---|
| Adults | | 7.3 | | |
| (♀) | | (3.6) | | |
| Eggs | | 738.5 | | |
| | Platygasterid | | 49.7 | 6.7 |
| | Predation (mainly *Cleobora mellyi*) | | 483.9 | 65.5 |
| Larvae 1-2 | | 204.9 | | |
| | *Eadya paropsidis* | | 70.9 | 34.6 |
| | Tachinids | | 6.4 | 3.1 |
| | Predation | | 73.0 | 35.6 |
| | Dispersal | | | |
| Larvae 3 | | 54.6 | | |
| | Tachinids | | 2.1 | 3.9 |
| | Predation | | 33.8 | 61.9 |
| | Dispersal | | | |
| Larvae 4 | | 18.7 | | |
| | Tachinids | | 0.3 | 1.5 |
| | Predation | | 5.1 | 27.3 |
| | Dispersal | | | |
| Pupae | | 13.3 | | |
| | | | 6.8 | 51.1 |
| Adults | | 6.5 | | |
| | | | 732.0 | 99.1 |

Larval mortality was very low in the first and second instars, which coincided with the period when the gregarious larval feeding habit was strongest. Attack of larvae by the parasitoid *Eadya paropsidis* occurred during these stages. High mortalities, most of which could not be attributed to a specific cause, occurred in the third and fourth instars. This larval "disappearance" represented a combination of factors including predation and active and passive emigration. It was not possible to gain a direct measure of larval predation, but larvae which were in the process of being consumed by *Cleobora mellyi* adults or larvae were occasionally encountered in the course of sampling. In the third instar, feeding groups began to split up as larvae moved further in search of food, and in this way they were both more available for predation, and more easily lost through active or passive emigration.

Larval parasitization by *Eadya paropsidis* was much greater than by the tachinid parasitoids (*Anagonia rufipes* and *Paropsivora* sp.) at East Ridgley, while the reverse situation applied at Bunkers Thinned. At this latter site, the tachinid factor acted with approximately equal severity in each stage.

Total mortalities from eggs to fourth instar larvae were similar in all three budgets, ranging from 97.5% (East Ridgley 1975/76) to 98.1% (East Ridgley 1974/75). Pupal mortality in the soil, due to unknown causes, accounted for just over 50 percent of pupae, bringing the total mortality from eggs to adults to 99.1% at East Ridgley, 1975/76. This mortality resulted in a slightly decreased population of teneral adults in the new generation, the ratio of new to old adults being 1:1.12. Assuming a 1:1 sex ratio (Section V.3.2.1.), parental generation females laid an average of 205 eggs per female over a period of approximately 20 days. This was equivalent to 10.3 eggs per female per day, or just under one batch per female every two days.

## 4. Discussion

The life history of *C. bimaculata* in N.W. Tasmania showed many similarities to the life history of this species described by Greaves (1966) in the Florentine Valley, S. Tasmania. The major discrepancy was that *C. bimaculata* had only one generation per season in N.W. Tasmania. Greaves based his assumption that *C. bimaculata* was bivoltine on his observation of two oviposition peaks each season in the Florentine Valley. This showed apparent similarity to Carne's (1966a) finding that the closely related species, *Paropsis atomaria*, was bivoltine in S.E. mainland Australia.

The bimodal pattern of oviposition did not always occur in N.W. Tasmania (Fig. 265). Where two distinct oviposition peaks did occur (Bunkers Thinned 1973/74 and 1974/75), there was not sufficient time between them for the second peak to be the result of a second generation. Greaves (*loc. cit.*) found that at a constant temperature of 15°C, which closely approximated summer mean field temperatures (Table 19), the total developmental time of the immature stages was 54 days. Adults emerging from pupae in the laboratory required at least eight days at 25°C for ovarian development and maturation to occur (Davies 1966). Therefore, an absolute minimum generation time for *C. bimaculata* in mid-summer would be of the order of 60 to 65 days. A time interval of this length was not observed between oviposition peaks at any site, or in any season (Fig. 265).

Jacobs (1955) showed that, as a result of insect defoliation, eucalypts may produce several flushes of foliage in a season. Second, and subsequent growth flushes, developed from accessory

Fig. 265. Percentage of shoots occupied by *C. bimaculata* eggs ( ▲-▲ ) and larvae ( ■-■ ) at Surrey Hills and East Ridgley study sites, 1973-76.

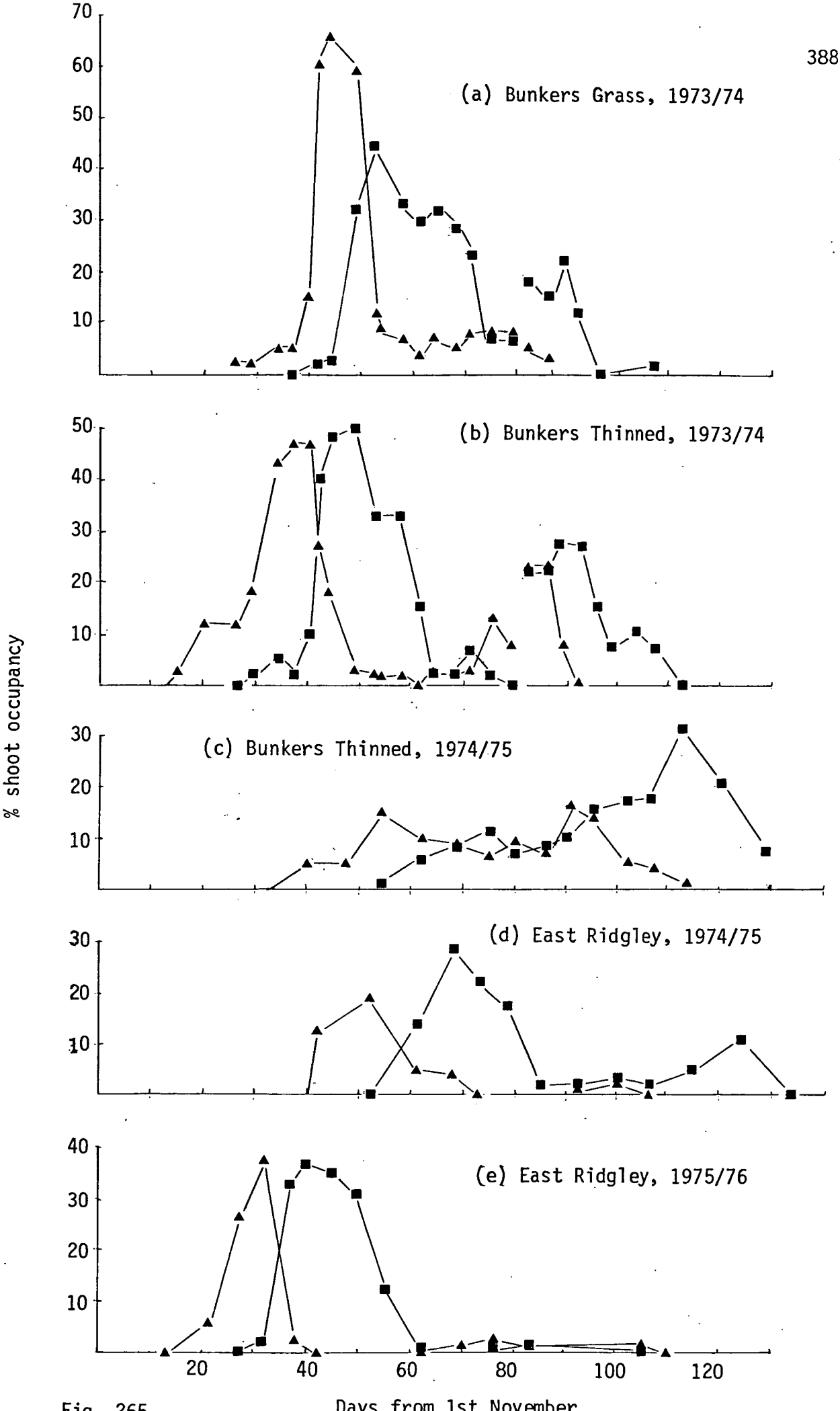
(a) Bunkers Grass, 1973/74
(b) Bunkers Thinned, 1973/74
(c) Bunkers Thinned, 1974/75
(d) East Ridgley, 1974/75
(e) East Ridgley, 1975/76
% shoot occupancy
Days from 1st November

Fig. 265

buds which were normally inhibited from developing in the absence of defoliation. The two peaks of oviposition were therefore attributable to one generation of adults responding to two flushes of food. Adults collected early in the season oviposited in the laboratory at a constant 23°C for up to 130 days (Fig. 254). Therefore, in the absence of predation, adults could be expected to survive in the field for at least a similar period.

Carne (1966a) proved that *P. atomaria* was bivoltine by weekly dissection and observation of the ovarian condition of a sample of females. A period occurred in mid-January when there were no females with mature ovaries (Fig. 266). When weekly collections of *C. bimaculata* females from East Ridgley were dissected, there was no indication of a mid-season break in the presence of mature ovaries.

The mature ovaries of surviving second year females held in the laboratory under natural light conditions regressed in a manner similar to that described by Waloff and Richards (1957) in the northern hemisphere chrysomeline species, *Phytodecta olivacea*. However, second year females of *C. bimaculata* did not constitute a significant proportion of the diapausing field population as they did with *Ph. olivacea*.

The life cycle of *C. bimaculata* in N.W. Tasmania is presented diagrammatically in Fig. 267. The overwintering phase, in which adults are in diapause, normally lasts for approximately eight months, while the active phase lasts for the remaining four months of the year. All adults undergo diapause before reaching sexual maturity. After the breaking of diapause, adults usually survive for most of the ensuing season, mating and ovipositing frequently.

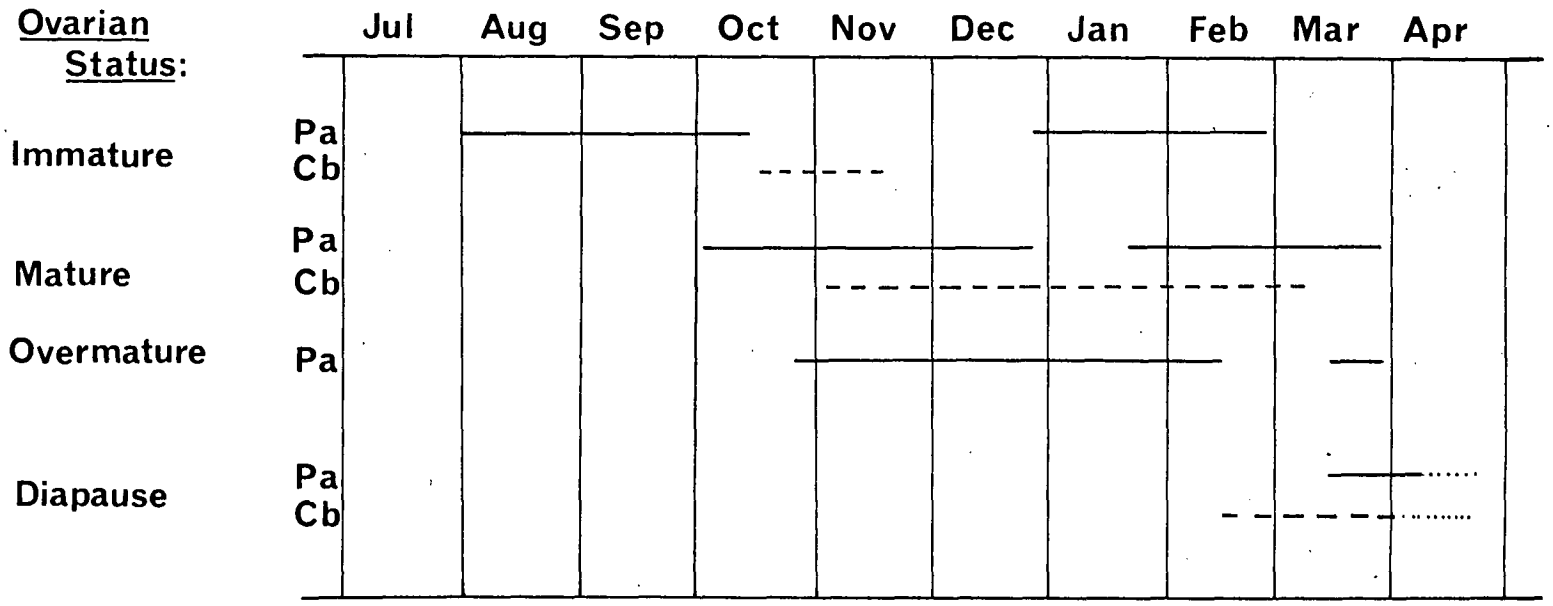


Fig. 266. Ovarian status of female *Paropsis atomaria* (Carne 1966a) (Pa) and *Chrysophtharta bimaculata* (present study) (Cb) adults throughout year.

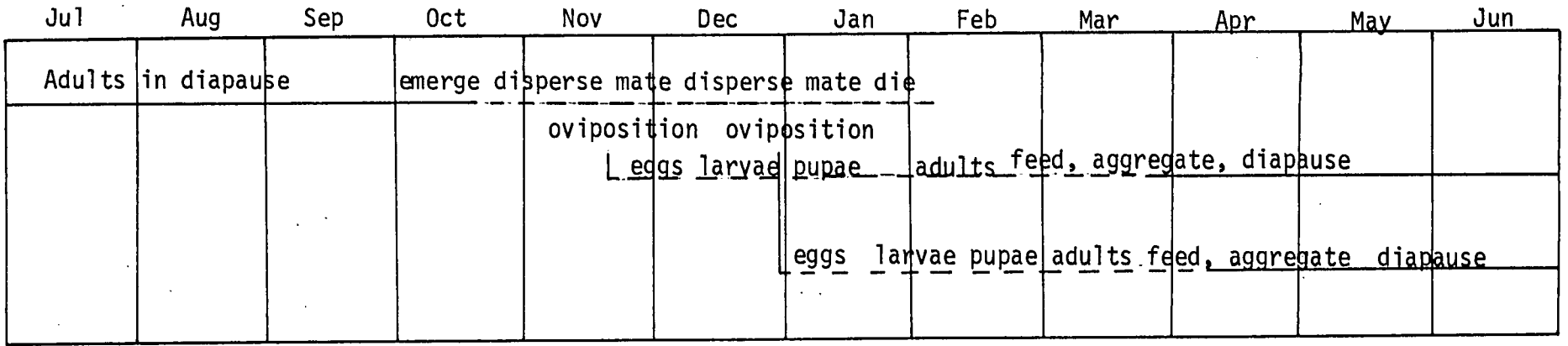


Fig. 267. Life cycle of *C. bimaculata*.

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Fig. 268. Feeding groups of *Chrysophtharta bimaculata* larvae on *E. regnans* leaf.

At any one site, there may be more than one peak of oviposition, depending on the condition of the foliage. That foliage condition may play an important role in the phenology of *C. bimaculata*, was indicated by the artificial production of two generations in one season in an outside wire-mesh insectary. The mesh of the insectaries provided a sheltered micro-habitat for the *E. delegatensis* seedlings planted in them, with the consequent early production of lush and abundant foliage. Oviposition in insectaries at Ridgley commenced seven weeks earlier than in the field at East Ridgley.

In spite of its uni-voltine life cycle, *C. bimaculata* closely resembles *Paropsis atomaria* in many aspects of its life history, biology and behaviour. Both species have a similar reproductive capacity and ovipositing females depend on the phenology of the host trees. *C. bimaculata* appears to be more dependent on the occurrence of unusually warm days, early in the season, for the initiation of major oviposition (as noted by Greaves (1966) and in the current study), than is *P. atomaria* (Carne 1966a). However, while maximum temperatures of 25°C to 30°C are rare in Tasmania, they are of more common occurrence in the Canberra region, where yet higher maxima, though of rarer occurrence, have a detrimental effect on *P. atomaria* field populations (Carne *loc. cit.*). Despite differing placement and arrangement of eggs in oviposition, the two paropsid species showed an identical spatial pattern of oviposition among shoots (Carne *loc. cit.*). Larvae of both *C. bimaculata* and *P. atomaria* show strong colonial group-feeding behaviour (Fig. 268), similar to that shown by larvae of the sawfly *Perga affinis affinis* (Carne 1962, 1966c). Carne (1968) considered that this phenomenon favoured greater survival of larvae

at moderately high rather than at low densities.

Field population studies at two major sites (East Ridgley and Bunkers Thinned, "Surrey Hills"), and ancillary observations, revealed the existence of a natural enemy complex of the immature stages similar to that reported for *Paropsis atomaria* (Tanton and Khan 1978). New egg and larval parasitoids recorded for *C. bimaculata* are the pteromalid, *Enoggerella nassaui* Girault, an unidentified inostemmatine platygasterid (both egg parasitoids) and *Eadya paropsidis* Huddleston, the braconid larval parasitoid recorded from *Paropsis atomaria* (Huddleston and Short 1978; Tanton and Khan *loc. cit.*). The fungal pathogen,*Metarhizium* sp., caused mortality of adults in overwintering sites.

Preparation of partial population budgets for populations of *C. bimaculata* revealed that among the immature stages, egg predation was a major mortality factor. The main egg predator was the coccinellid *Cleobora mellyi* Mulsant, adults and larvae of which preyed on eggs and larvae of the host. Laboratory feeding trials revealed that while eggs of *C. bimaculata* are a complete food for *Cl. mellyi*, the coccinellid cannot survive on a diet consisting entirely of *C. bimaculata* larvae. However, *Cl. mellyi* larvae may complete their development, and adults may survive for short periods on this food alone. Much of the larval "disappearance" shown in the budgets was undoubtedly due to predation of larvae by *Cl. mellyi*, a phenomenon frequently observed, but of which no evidence was left. When eggs of *C. bimaculata* are not present, essential dietary factors for *Cl.mellyi* may be derived from alternate food sources, e.g. the psyllid *Glycaspis* sp.

Larval "disappearance", i.e. mortality attributable to predation and active and passive emigration, was greatest in the third instar stage. Third instar larvae ingest greatly increased quantities of food than previous instars (Carne 1966b) and, accordingly, this stage is accompanied by increased movement and break-up of feeding colonies as new, suitable foliage is sought. Also at this stage, the relatively larger larvae are more evident,and hence available, to avian predators.

Parasitization accounted for a considerable proportion of larval mortality. Incidence of braconid (*Eadya paropsidis*) parasitization was much greater at East Ridgley, while the tachinids (*Anagonia rufipes* and *Paropsivora* sp.) predominated at Bunkers Thinned. The braconid was possibly less well adapted to the environmental extremes of the latter higher altitude site, while in the milder East Ridgley site it competitively displaced the tachinids.

The superior competitive ability of the braconid parasitoid in less climatically extreme habitats was due to its ability to attack and successfully parasitize very young larvae. The early establishment of the strongly mandibulate braconids in their hosts presumably conferred competitive advantage over subsequent development of tachinid maggots.

Since *C. bimaculata* adults were observed to disperse widely between overwintering sites and areas where feeding, oviposition, and development of the immature stages took place, it was not possible to follow a discrete population through a number of consecutive generations. The overall population trend observed in N.W. Tasmania over a period of six seasons has been one of decline. There was a rapid early decline from the "outbreak"

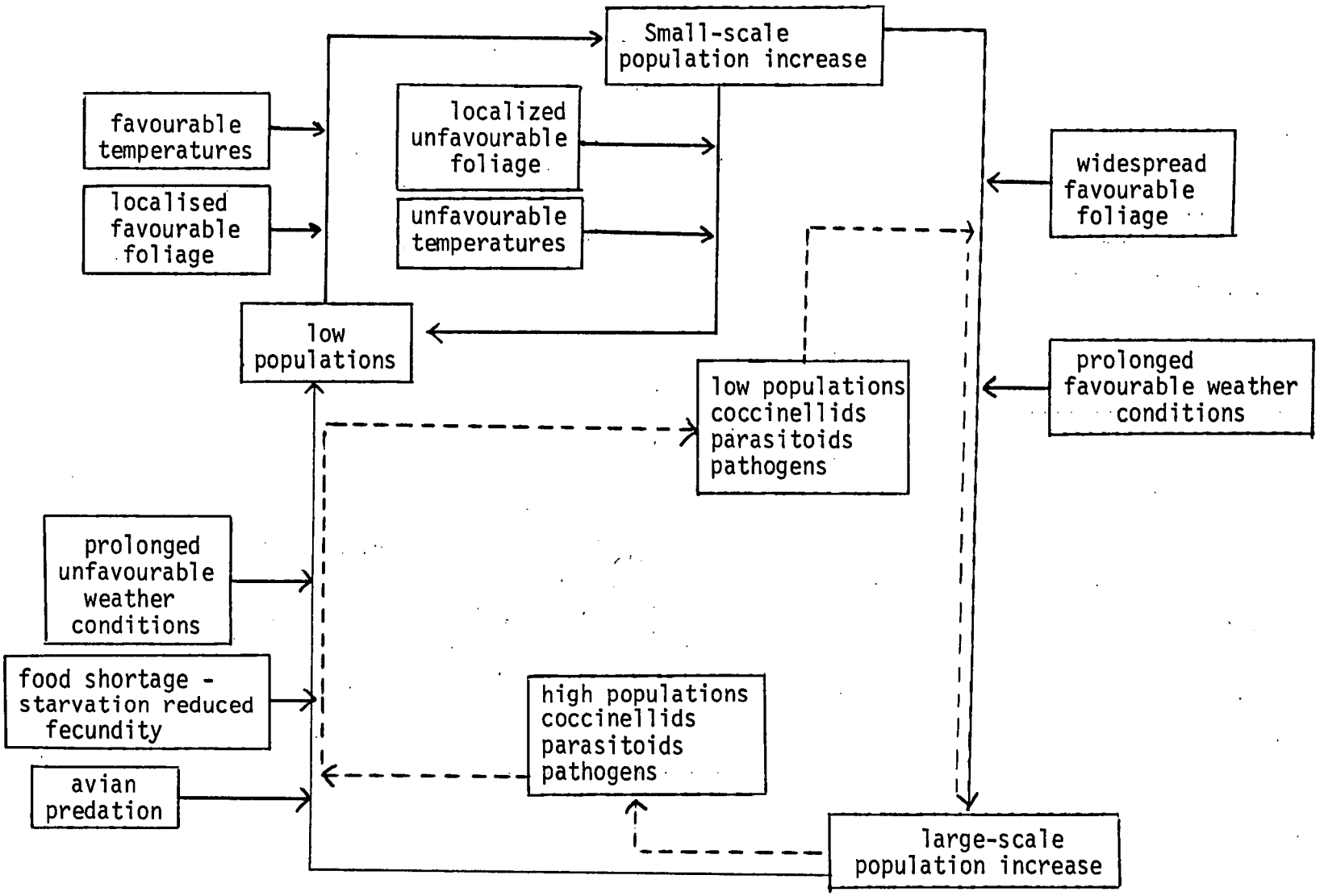
situation reported in "Surrey Hills" in 1972 and 1973 (D. de Boer *pers. comm.*). Populations were moderately large in the 1973/74 season but were much smaller in 1974/75 and by 1975/76 had declined to a marginally detectable level at which they remained for the succeeding seasons. At East Ridgley, observations were made on a plantation of *E. regnans* established in 1971. A small population of *C. bimaculata* was observed on these trees in the 1973/74 season, but in the two following seasons populations were much larger, causing extensive defoliation. In the 1976/77 season, and succeeding seasons, the population was again small.

Availability of favourable host foliage therefore seems to be a major regulator of population size. Young trees appear to pass through a phase when their foliage is favourable for *C. bimaculata*. In the case of vigorously growing plantation trees, such as the East Ridgley *E. regnans*, this phase is quickly passed, while it is probably protracted in slower growing natural regeneration situations such as in "Surrey Hills".

Under outbreak conditions, when the controlling function of the natural predator/parasitoid complex breaks down, and there is a shortage of favourable foliage, the population may "over-flow" on to less favourable foliage on mature trees. Kile (1974) recorded substantial attack of mature (60 year-old) *E. obliqua* and *E. regnans* stands in southern Tasmania during population outbreak.

The major factors in the life system of *C. bimaculata* are summarized in Fig. 269. Under normal circumstances populations appear to be maintained at a low level by the availability of favourable foliage, and, to a lesser extent, by the natural

Fig. 269. Life system of *Chrysophtharta bimaculata*.



predator/parasitoid/pathogen complex. Local population"build-ups" may occur in the presence of favourable foliage when spring and summer weather conditions are favourable. If a large quantity of suitable foliage is available in the form of extensive uniform monospecific young regeneration stands, and weather is favourable over several seasons (i.e. average rainfall and warm, settled spring/summer seasons), population outbreak may be initiated. Under these conditions the population may ultimately be controlled by a combination of the factors of reduced survival and fecundity on less favourable foliage, avian predation, unfavourable weather over two or more years, and increased populations of coccinellid predators, parasitoids and pathogens.

# SECTION VI - GENERAL DISCUSSION AND CONCLUSION

General discussion and conclusion

Prior to the commencement of this study, the number, identification and distribution of the *Eucalyptus*-defoliating paropsid beetles in Tasmania was largely unknown. One species, *Chrysophtharta bimaculata* (Olivier), was reported as a pest of forest regeneration in the Florentine Valley of southern Tasmania (Greaves 1966). The increasing demands placed on Tasmania's forest resources since the late 1960's has led to an intensification of forest regeneration practices. Between 1968 and 1972 there were reports of defoliation of regeneration due to paropsids in the southern forests (J.L. Madden, *pers. comm.*), the Mersey Valley (K.L. Taylor, *pers. comm.*), and the north western forests (D. de Boer, *pers. comm.*). An understanding of the identity and ecology of potential forests pests has become more essential since the commencement of large scale clear-felling and regeneration establishment associated with the export wood-chip industry.

A survey of eucalypt forest and woodlands throughout most of the island revealed the existence of at least 36 paropsid species which fed on foliage of eucalypts. The identity of most of these species was confirmed by rearing them through all stages in the laboratory, and by undertaking morphological studies of egg, larvae and adult stages.

The species were identified as belonging to five genera, *viz*: *Paropsis* Olivier, *Trachymela* Weise, *Chrysophtharta* Weise, *Paropsisterna* Motschulsky, and *Sterromela* Weise. Due to the current state of nomenclatural confusion within the paropsid group (B.J. Selman 1963, and *pers. comm.*) it has been possible to positively identify only 23 species. No attempt has been made to

erect new species, since it is felt that in the absence of a recent revision of the entire paropsid fauna, nomenclatural confusion could be greatly increased. Instead, all species have been identified to the generic level, which in most cases is unambiguous, and within each genus, all species have been assigned a code number. The only nomenclatural change to be made has been the transfer of *Paropsisterna lineata* (Marsham) to the genus *Sterromela*.

In comparison with the entire paropsid fauna, the Tasmanian fauna appears rich in species of *Chrysophtharta*, and impoverished with respect to species of *Trachymela*. The isolation of Tasmania from mainland Australia by the substantial biological barrier of Bass Strait for the past 12,000 years, together with probable partial isolation before this time, and a generally wetter and cooler climate than that of mainland Australia, has led to the evolution of a distinct Tasmanian paropsid fauna. However, there are close affinities with the fauna of mainland south-eastern Australia. Endemic Tasmanian species, often have closely related allopatric species in the mainland south-east, e.g. *Paropsis incarnata* Erichson and *P. atomaria* Olivier.

While surveying the Tasmanian paropsid fauna on eucalypts, it was observed that species differed regarding catholicity of host species range. While many species (e.g. *Chrysophtharta bimaculata, C. agricola, Paropsis charybdis*) were usually found only on eucalypts within a distinct sub-generic taxon, others (e.g. *Chrysophtharta nobilitata, Paropsis aegrota, P. porosa*) were collected from the full taxonomic range of eucalypts in Tasmania. Apparent relative lack of host specificity of the *Eucalyptus*-defoliating paropsids contrasts strongly with the host-plant relationships of the North American chrysomelids

(Brown 1956, 1959), and is an indication of the close affinities and genetic plasticity within the genus *Eucalyptus* in which evolution is proceeding rapidly at the current time (Pryor 1959). Sampling of populations of species on young trees at regular intervals throughout summer seasons revealed that apparent cases of niche overlap between species were rare. In general, species feeding on the same host were phenologically well separated. However, the fact that examples of niche overlap were observed is an indication that evolution may be proceeding at a fast rate among the paropsids themselves.

While some species were always only encountered in low numbers, other species were often locally extremely abundant, causing significant defoliation damage to young trees. These latter, more prominent species showed all the characteristics of high "r"-selection (Macarthur and Wilson 1967) including high fecundity and intensely gregarious larvae which showed colonial, group-feeding behaviour. Such species appeared to predominate in the relatively unstable, disturbed and transient ["ruderal" - Grime (1978)] habitats of young eucalypt regrowth. Hence they were the potential pests of young commercially regenerated forests and of plantations.

Experimental rearing of larvae of two common, highly "r"-selected species with similar phenologies, *Chrysophtharta bimaculata* and *C. agricola*, revealed that the latter species was competitively displaced from an inherently favourable host (*E. delegatensis*) by *C. bimaculata*. Although a less efficient feeder, *C. bimaculata* had a slightly shorter larval duration, and was therefore the more highly "r"-selected species. Laboratory feeding tests with *C. bimaculata* and *C. agricola* on a range of hosts revealed that while completion of development on each host tested was possible, some hosts were inherently much less favourable than others. The

essential oils which occur in eucalypts [listed by Penfold and Willis (1961)] may play an important role in the determination of host preferences.

Because of the pest status of *C. bimaculata* on commercially important eucalypts in Tasmania, a detailed study of the life history and population biology of this species was undertaken. Populations of *C. bimaculata* were present in outbreak proportions on *E. delegatensis* regeneration in "Surrey Hills" at the commencement of this study, but rapidly declined to normal levels over a two year period. Many of the findings of Greaves (1966) in the Florentine Valley were borne out in this study, however a major discrepance was the number of generations of *C. bimaculata* per annum.

After regular sampling of populations in the initial season of study (1973/74), it was found that although *C. bimaculata* sometimes had bimodal oviposition peaks, as was also recorded by Greaves (*loc. cit.*) in the Florentine Valley, this was not the result of two distinct generations of adults in the one season, as interpreted by Greaves. A second oviposition peak was the result of suppressed shoots becoming attractive for oviposition after defoliation of dominant shoots by larvae resulting from an initial large oviposition early in the season.

The fixed tag method of sampling employed by Carne (1966a) for sampling populations of *Paropsis atomaria*, was abandonned after the 1973/74 season because of the variability of individual shoot units throughout the season and a system of destructive sampling was employed. This system had the advantage that it enabled a sampling of a far larger area at each study site, it enabled detailed counts to be made in the relative comfort of the

laboratory, and it enabled a study of parasitization to be carried out concurrently with the population sampling. The sampling method was designed to give a sample standard error of ten percent of the sample mean when the population of each stage was at peak levels. This objective proved difficult to achieve as populations declined.

The preparation of accurate stage-specific population budgets from a series of population samples taken at successive time intervals is recognised to be a difficult procedure since it requires an estimate of total recruitment to each stage. Southwood and Jepsons' (1962) method of integrating areas under stage population curves gives a value approximating to the total population at the median age of the stage. However, if there is a heavy and constant mortality which cannot be accounted for, this total population estimate will deviate from the actual stage recruitment. Since the commencement of the current study, several computer methods have been published which estimate total stage recruitment (Manly 1974a, b; Ruesink 1975; Birley 1977). These methods allow for a more flexible sampling programme, in which frequency of sampling assumes relatively more importance, but accuracy of samples is far less important. When sampling data from East Ridgley in the 1975/76 season was analysed using the Manly method, sampling points in each stage were too few to allow any improvement of estimate precision on Southwood and Jepsons' graphical method (M. Birley, *pers. comm.*). In order for the computer methods to be applicable in *C. bimaculata* population studies, a programme of daily sampling would be required.

Three partial population budgets were constructed using Southwood and Jepsons' method for estimating stage recruitment. These budgets showed egg and larval predation due to the predatory

coccinellid species *Cleobora mellyi*, to be a major mortality factor in populations of immature *C. bimaculata*. Larval parasitization by two tachinid and one braconid species were also significant mortality factors. Due to the dispersive behaviour of *C. bimaculata* adults between oviposition sites and overwintering sites, it was not possible to follow discrete populations through several generations and undertake key factor studies. A consideration of population trends in study areas over a period of five consecutive seasons together with behavioural observations in the field indicated that foliage favourability and weather conditions were also major population determinants (Fig. 268), although much more work is required to describe their precise functions.

In general, other *Eucalyptus*-defoliating paropsid species in Tasmania do not appear to be as prone to widespread population outbreak as *C. bimaculata*. The relative instability of *C. bimaculata* populations may be explained by the ecological strategy employed by its preferred hosts of the subgenus *Monocalyptus*, series Obliquae. Most species of eucalypts are resistant to intense fires, recovering from burning by sprouting epicormic buds and coppice shoots from lignotubers. However, species of the series Obliquae are killed by intense fires, but due to their high seeding capacity, heavy seeding into ash-beds occurs after a hot burn. Since most of the undergrowth vegetation is killed by the fire, a dense, monospecific seedling stand results. This provides an ecologically unstable and ruderal habitat which favours the most highly "r"-selected of insect grazers. *C. bimaculata* was shown to be more highly "r"-selected than the closely related species *C. agricola*, the preferred hosts of which are the more fire-resistant *Symphyomyrtus* species. These eucalypts tend to

occur in mixed stands with other fire-resistant *Monocalyptus* species.

To date, eucalypt species of the series Obliquae have been the most commercially sought species in Tasmania. This had led to the clear-felling and regeneration of many stands of *E. obliqua*, *E. regnans* and *E. delegatensis*. The method of regeneration most commonly employed has been the burning of logging slash, followed by aerial seeding of the same species on to the ash-bed. This regeneration technique closely mimics the natural ecological strategy of the Obliquae species. The result of these practices, in areas such as the Florentine Valley of southern Tasmania, has been to maintain a succession of large, young monospecific regeneration stands highly attractive to *C. bimaculata*. This undoubtedly accounts for the high populations of *C. bimaculata* continually observed in the Florentine Valley (H.J. Elliott, *pers. comm.*). In the higher altitude *E. delegatensis* forests of N.W. Tasmania, this regeneration system has not been followed as intensively as in the Florentine Valley, and, with the environment unfavourable for overwintering populations of *C. bimaculata*, population outbreak appears to be a far less frequent phenomenon. Although *C. bimaculata* is always likely to remain a major forest pest in Tasmania due to the preference of the forest industry for species of the series Obliquae, recent trends in large-scale planting of other species, especially the *Symphyomyrtus* species *E. globulus* and *E. nitens*, may possibly promote the emergence of other highly "r"-selected paropsid species as major pests.

The approach in this initial study of the *Eucalyptus*-defoliating paropsids in Tasmania has been broad, incorporating the aspects of taxonomy, bionomics, general ecology and

population ecology. While detailed studies in each field covered have necessarily been limited by this approach, it has been possible to draw broad conclusions regarding the relationships between species and their hosts, and the functioning of a life system. However, considerably more detailed studies are required in all aspects considered to fully elucidate relationships and the functioning of systems. In particular, with ever-increasing demands being placed on forest resources, a thorough knowledge of the taxonomy and bionomics of the insect fauna associated with eucalypts, of which the defoliating paropsids are an important component, is essential.

# SECTION VII - REFERENCES

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# APPENDICES

APPENDIX 1.

Percentage of shoots occupied by immature stages of larvae of *Chrysophtharta* spp. on successive sampling dates in the 1973/74 season (three-date running averages).

1. Ridgley: *E. gunnii* (25 shoots)

| Date | *C. agricola* | *C. variicollis* |
|---|---|---|
| 12.xi.73 | 64 | 4 |
| 19.xi.73 | 69 | 7 |
| 20.xi.73 | 73 | 8 |
| 27.xi.73 | 75 | 8 |
| 30.xi.73 | 77 | 8 |
| 5.xii.73 | 76 | 7 |
| 9.xii.73 | 71 | 7 |
| 12.xii.73 | 59 | 5 |
| 15.xii.73 | 39 | 5 |
| 20.xii.73 | 21 | 3 |
| 24.xii.73 | 7 | 1 |
| 2.i.74 | 3 | 1 |
| 9.i.74 | | 5 |
| 16.i.74 | 3 | 12 |
| 24.i.74 | 3 | 21 |
| 30.i.74 | 4 | 28 |
| 8.ii.74 | 4 | 40 |
| 13.ii.74 | 4 | 49 |
| 18.ii.74 | 5 | 57 |
| 22.ii.74 | 5 | 52 |
| 26.ii.74 | 9 | 37 |
| 4.iii.74 | 9 | 24 |
| 11.iii.74 | 8 | 20 |

APPENDIX 1 (continued)

2. "Surrey Hills": *E. delegatensis* (60 shoots)

| Date | *C. nobilitata* | *C. bimaculata* |
|---|---|---|
| 15.xi.73 | 4 | |
| 20.xi.73 | 7 | |
| 26.xi.73 | 9 | 1 |
| 29.xi.73 | 9 | 3 |
| 4.xii.73 | 8 | 4 |
| 7.xii.73 | 8 | 8 |
| 10.xii.73 | 8 | 27 |
| 12.xii.73 | 8 | 47 |
| 14.xii.73 | 7 | 62 |
| 19.xii.73 | 5 | 57 |
| 23.xii.73 | 3 | 51 |
| 24.xii.73 | 1 | 43 |
| 28.xii.73 | 2 | 38 |
| 31.xii.73 | 3 | 35 |
| 3.i.74 | 3 | 33 |
| 7.i.74 | 3 | 32 |
| 10.i.74 | 1 | 24 |
| 14.i.74 | | 18 |
| 18.i.74 | | 14 |
| 21.i.74 | | 16 |
| 25.i.74 | | 20 |
| 28.i.74 | | 17 |
| 31.i.74 | | 14 |
| 4.ii.74 | | 6 |
| 7.ii.74 | | 2 |
| 11.ii.74 | | 1 |
| 15.ii.74 | | 1 |

APPENDIX 2

Larval feeding trial 1: Survival, rate of growth, rate of food consumption and conversion ratios of *C. bimaculata* and *C. agricola* larvae reared on foliage of *E. delegatensis* and *E. dalrympleana*.

1. Survival until prepupal stage

Each replicate culture initially contained 25 larvae.

| | Replicates | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | Total |
| *C. bimaculata* - *E. delegatensis* | 17 | 21 | 20 | 23 | 81 |
| *C. bimaculata* - *E. dalrympleana* | 13 | 10 | 10 | 17 | 50 |
| *C. agricola* - *E. delegatensis* | 10 | 17 | 18 | 22 | 67 |
| *C. agricola* - *E. dalrympleana* | 18 | 22 | 22 | 22 | 84 |

APPENDIX 2 (continued)

2. Duration of larval feeding stage (days)

2.1. *C. bimaculata* - *E. delegatensis*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 12 | 12 | 12 | 12 |
| | 12 | 12 | 12 | 12 |
| | 12 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 13 | 13 |
| | 14 | 13 | 13 | 13 |
| | 14 | 13 | 13 | 13 |
| | 15 | 13 | 13 | 13 |
| | | 13 | 13 | 13 |
| | | 13 | 13 | 13 |
| | | 13 | 13 | 13 |
| | | 16 | 13 | 14 |
| | | 16 | 15 | 14 |
| | | 17 | | 14 |
| | | | | 15 |
| | | | | 15 |
| $\bar{x}$: | 13.18 | 13.19 | 12.65 | 13.04 |
| $\bar{x}^{-1}$: | | 13.02 | | |
| $S\bar{x}^{-1}$: | | 0.13 | | |

2.2. *C. bimaculata* - *E. dalrympleana*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 14 | 15 | 14 | 14 |
| | 15 | 15 | 15 | 15 |
| | 15 | 16 | 15 | 15 |
| | 16 | 16 | 16 | 16 |
| | 16 | 16 | 16 | 16 |
| | 16 | 19 | 17 | 16 |
| | 17 | 21 | 19 | 16 |
| | 17 | 22 | 19 | 16 |
| | 17 | 22 | 19 | 17 |
| | 17 | 24 | 20 | 17 |
| | 19 | | | 17 |
| | 20 | | | 17 |
| | 21 | | | 19 |
| | | | | 19 |
| | | | | 19 |
| | | | | 19 |
| | | | | 23 |
| $\bar{x}$: | 16.92 | 18.60 | 17.00 | 17.12 |
| $\bar{x}^{-1}$: | | 17.41 | | |
| $S\bar{x}^{-1}$: | | 0.40 | | |

APPENDIX 2 (continued)

2. Duration of larval feeding stage (days) (continued)

2.3. *C. agricola* - *E. delegatensis*

| Rep. 1 | 2 | 3 | 4 |
|---|---|---|---|
| 15 | 15 | 15 | 15 |
| 15 | 15 | 15 | 15 |
| 15 | 15 | 15 | 15 |
| 15 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 19 | 16 | 16 | 15 |
| | 16 | 16 | 15 |
| | 16 | 16 | 15 |
| | 16 | 17 | 16 |
| | 16 | 17 | 16 |
| | 16 | 17 | 16 |
| | 17 | 20 | 16 |
| | 20 | 20 | 16 |
| | | 20 | 16 |
| | | | 16 |
| | | | 16 |
| | | | 16 |
| | | | 17 |
| $\bar{x}$: | 15.90 | 16.12 | 16.67 | 15.50 |
| $\bar{x}^1$: | | 16.05 | | |
| $S_{\bar{x}}{}^1$: | | 0.24 | | |

2.4. *C. agricola* - *E. dalrympleana*

| Rep. 1 | 2 | 3 | 4 |
|---|---|---|---|
| 16 | 15 | 15 | 15 |
| 16 | 15 | 15 | 15 |
| 16 | 15 | 15 | 15 |
| 16 | 15 | 15 | 15 |
| 16 | 15 | 16 | 15 |
| 16 | 15 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 16 | 16 | 16 | 15 |
| 17 | 16 | 16 | 16 |
| 17 | 16 | 16 | 16 |
| 17 | 16 | 16 | 16 |
| 20 | 17 | 16 | 16 |
| 20 | 17 | 17 | 16 |
| 20 | 17 | 17 | 16 |
| 20 | 17 | 17 | 17 |
| 20 | 17 | 17 | 17 |
| 21 | 17 | 17 | 17 |
| | 19 | 17 | 17 |
| | 19 | 17 | 17 |
| | 19 | 19 | 17 |
| | 20 | 21 | 17 |
| $\bar{x}$: | 17.56 | 16.59 | 16.50 | 15.91 |
| $\bar{x}^1$: | | 16.64 | | |
| $S_{\bar{x}}{}^1$: | | 0.34 | | |

APPENDIX 2 (continued)

3. Mass of adults (mg)

3.1. *C. bimaculata* - *E. delegatensis*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 47.9 | 47.8 | 48.1 | 41.7 |
| | 47.6 | 38.7 | 45.3 | 54.1 |
| | 42.1 | 44.6 | 50.0 | 38.1 |
| | 37.1 | 53.3 | 50.0 | 46.1 |
| | 44.9 | 46.6 | 46.1 | 38.8 |
| | 36.1 | 44.6 | 41.3 | 37.6 |
| | 40.7 | 37.8 | 45.0 | 44.6 |
| | 37.9 | 48.3 | 47.8 | 51.7 |
| | 39.9 | 33.6 | 45.3 | 36.4 |
| | 42.2 | 38.4 | 41.0 | 39.5 |
| | 48.9 | 50.9 | 41.5 | 39.9 |
| | 34.4 | 38.8 | 54.8 | 40.8 |
| | 35.5 | 36.4 | 49.1 | 37.1 |
| | 46.2 | 34.6 | 43.6 | 44.5 |
| | 39.5 | 48.3 | 41.0 | 32.4 |
| | 35.8 | 46.7 | 33.3 | 38.8 |
| | 42.1 | 32.0 | 32.5 | 43.6 |
| | | 33.1 | 38.8 | 33.2 |
| | | 23.1 | | |

$\bar{x}$: 41.25

$S\bar{x}$: 0.89

(n = 72)

3.2. *C. bimaculata* - *E. dalrympleana*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 46.5 | 48.3 | 40.6 | 47.0 |
| | 36.6 | 39.0 | 44.4 | 51.8 |
| | 35.6 | 37.1 | 38.2 | 50.8 |
| | 42.2 | 29.3 | 35.4 | 46.4 |
| | 43.9 | 41.6 | 42.5 | 49.9 |
| | 43.4 | 45.2 | 46.5 | 46.4 |
| | 41.0 | 36.6 | 40.8 | 45.6 |
| | 42.3 | 42.2 | 48.3 | 47.0 |
| | 38.3 | 39.2 | | 49.3 |
| | 44.5 | | | 40.4 |
| | 45.6 | | | 50.0 |
| | 44.6 | | | 48.4 |
| | | | | 43.6 |
| | | | | 45.6 |
| | | | | 42.4 |

$\bar{x}$: 43.28

$S\bar{x}$ : 0.72

(n = 44)

APPENDIX 2 (continued)

3. Mass of adults (mg) (continued)

3.3. *C. agricola* - *E. delegatensis*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 41.2 | 55.7 | 45.2 | 46.3 |
| | 45.6 | 49.0 | 37.8 | 41.8 |
| | 33.2 | 43.6 | 45.3 | 32.2 |
| | 33.4 | 37.0 | 37.2 | 44.3 |
| | 42.4 | 40.7 | 41.6 | 38.7 |
| | 37.0 | 34.7 | 37.0 | 46.2 |
| | 39.1 | 38.2 | 47.0 | 32.5 |
| | 38.5 | 36.6 | 37.1 | 39.3 |
| | 43.0 | 31.7 | 43.2 | 51.5 |
| | 36.0 | 43.0 | 33.5 | 49.1 |
| | | 46.8 | 33.4 | 42.4 |
| | | 36.4 | 39.4 | 37.9 |
| | | 39.0 | 43.2 | 42.9 |
| | | 40.0 | 44.3 | 49.0 |
| | | 32.8 | 37.3 | 33.0 |
| | | 35.2 | 44.6 | 51.4 |
| | | | 26.6 | 38.6 |
| | | | | 38.6 |
| | | | | 38.9 |
| | | | | 47.1 |
| | | | | 35.4 |

$\bar{x}$: 40.32

$S\bar{x}$: 0.71

(n = 64)

*C. agricola* - *E. dalrympleana*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 40.9 | 34.8 | 39.5 | 48.6 |
| | 44.8 | 43.3 | 41.5 | 40.8 |
| | 45.0 | 38.5 | 36.8 | 41.7 |
| | 37.2 | 44.6 | 47.0 | 37.1 |
| | 44.6 | 47.2 | 39.0 | 39.9 |
| | 52.7 | 45.5 | 41.7 | 48.7 |
| | 39.4 | 43.3 | 42.0 | 33.0 |
| | 39.8 | 47.8 | 41.0 | 56.8 |
| | 36.1 | 40.0 | 37.9 | 35.3 |
| | 43.9 | 47.7 | 42.5 | 43.1 |
| | 45.3 | 42.0 | 38.6 | 44.4 |
| | 45.3 | 41.8 | 46.2 | 46.3 |
| | 49.4 | 44.1 | 46.1 | 41.8 |
| | 45.5 | 41.9 | 38.4 | 44.1 |
| | 36.0 | 53.9 | 33.9 | 45.5 |
| | 41.4 | 49.2 | 38.7 | 38.1 |
| | | 45.7 | 45.7 | 55.3 |
| | | 40.3 | 42.8 | 40.9 |
| | | 42.3 | 26.8 | 46.7 |
| | | | 49.1 | 40.7 |
| | | | | 43.6 |
| | | | | 48.8 |
| | | | | 49.3 |

$\bar{x}$: 42.91

$S\bar{x}$: 0.58

(n = 78)

APPENDIX 2 (continued)

4. Fresh mass of foliage consumed per larva (mg)

4.1. *C. bimaculata - E. delegatensis*

| Day | Replicate 1 | 2 | 3 | 4 | Mean | Cumulative Mean |
|---|---|---|---|---|---|---|
| 1 | | 0.46 | 1.90 | 0.78 | 0.54 | |
| 2 | 0.96 | 3.92 | 3.81 | 3.98 | 3.17 | 3.95 |
| 4 | 6.06 | 5.43 | 6.55 | 5.23 | 5.82 | 9.77 |
| 5 | 8.28 | 9.32 | 12.47 | 9.83 | 9.98 | 19.75 |
| 7 | 13.59 | 18.93 | 20.67 | 22.87 | 19.02 | 38.77 |
| 8 | 30.47 | 30.30 | 39.57 | 36.84 | 34.29 | 73.06 |
| 9 | 35.55 | 40.94 | 47.79 | 41.67 | 41.49 | 114.55 |
| 10 | 72.95 | 60.15 | 81.22 | 63.50 | 69.45 | 184.00 |
| 11 | 58.53 | 52.61 | 58.22 | 52.44 | 55.45 | 239.45 |
| 12 | 37.84 | 37.63 | 28.47 | 33.90 | 34.46 | 273.91 |
| 13 | 28.97 | 53.04 | 26.63 | 32.08 | 35.18 | 309.09 |
| 14 | 25.45 | 43.24 | 71.07 | 43.09 | 45.71 | 354.80 |
| 15 | 19.32 | 58.03 | 72.03 | 44.07 | 48.36 | 403.16 |
| 16 | | 44.25 | | | 11.06 | 414.22 |
| Total: | 337.97 | 458.21 | 470.40 | 390.28 | $S_{\bar{x}}$: | 30.93 |

APPENDIX 2 (continued)

4. Fresh mass of foliage consumed per larva (mg) (continued)

4.2. *C. bimaculata - E. dalrympleana*

| | Replicate | | | | | |
|---|---|---|---|---|---|---|
| Day | 1 | 2 | 3 | 4 | Mean | Cumulative Mean |
| 1 | | 0.79 | 1.79 | 2.00 | 1.15 | |
| 2 | 1.66 | 1.89 | 0.08 | 2.34 | 1.49 | 2.64 |
| 4 | 3.64 | 1.42 | 4.81 | 1.66 | 2.88 | 5.52 |
| 5 | 3.05 | 6.61 | 1.74 | | 2.84 | 8.32 |
| 7 | 5.29 | 9.01 | 7.41 | 6.22 | 6.98 | 15.35 |
| 8 | 9.71 | 5.81 | 5.47 | 13.22 | 8.55 | 23.90 |
| 9 | 13.08 | 6.17 | 3.23 | 5.62 | 7.03 | 30.93 |
| 10 | 24.85 | 13.22 | 12.12 | 18.01 | 17.05 | 47.97 |
| 11 | 24.79 | 13.36 | 10.62 | 21.62 | 17.60 | 65.57 |
| 12 | 20.07 | 13.03 | 11.06 | 22.23 | 16.60 | 82.17 |
| 13 | 32.30 | 68.73 | 27.69 | 33.81 | 40.63 | 122.80 |
| 14 | 35.40 | 39.51 | 36.13 | 51.34 | 40.60 | 163.39 |
| 15 | 45.78 | 22.37 | 17.55 | 51.02 | 34.18 | 197.57 |
| 16 | 53.19 | 19.60 | 75.08 | 46.45 | 48.58 | 246.15 |
| 17 | 53.95 | 62.09 | 34.21 | 50.36 | 50.15 | 296.30 |
| 19 | 42.74 | | | | 10.69 | 306.99 |
| 20 | | 34.38 | 11.55 | 9.82 | 13.94 | 320.93 |

..../continued over

APPENDIX 2 (continued)

4. Fresh mass of foliage consumed per larva (mg) (continued)

4.2. *C. bimaculata - E. dalrympleana* (continued)

| | Replicate | | | | | |
|---|---|---|---|---|---|---|
| Day | 1 | 2 | 3 | 4 | Mean | Cumulative Mean |
| 21 | | 59.87 | 36.30 | 73.43 | 42.40 | 363.33 |
| 22 | | 23.02 | | 64.95 | 21.99 | 385.32 |
| | | 108.56 | | 77.33 | 46.47 | 431.79 |
| 24 | | 60.04 | | | 15.01 | 446.80 |
| Total: | 369.50 | 569.48 | 296.84 | 551.43 | $S\bar{x}$: | 67.37 |

APPENDIX 2 (continued)

4. Fresh mass of foliage consumed per larva (mg) (continued)

4.3. *C. agricola - E. delegatensis*

| | Replicate | | | | | |
|---|---|---|---|---|---|---|
| Day | 1 | 2 | 3 | 4 | Mean | Cumulative Mean |
| 1 | 2.03 | 0.19 | 0.53 | 2.65 | 1.30 | |
| 2 | 2.15 | | 2.92 | 3.29 | 2.09 | 3.39 |
| 4 | 3.91 | 4.11 | 3.20 | 2.33 | 3.39 | 6.78 |
| 5 | 5.38 | 5.81 | 3.53 | 7.89 | 5.65 | 12.44 |
| 7 | 4.63 | 8.52 | 6.27 | 7.35 | 6.69 | 19.13 |
| 8 | 10.69 | 10.84 | 11.72 | 23.68 | 14.23 | 33.36 |
| 9 | 13.19 | 13.54 | 12.37 | 29.45 | 17.14 | 50.50 |
| 10 | 22.63 | 23.22 | 20.86 | 31.86 | 24.64 | 75.14 |
| 11 | 18.00 | 22.42 | 22.83 | 46.50 | 27.44 | 102.58 |
| 12 | 27.06 | 27.49 | 28.02 | 60.84 | 35.85 | 138.43 |
| 13 | 59.10 | 49.03 | 54.07 | 78.37 | 60.14 | 198.58 |
| 14 | 72.44 | 73.79 | 65.65 | 64.85 | 69.19 | 267.76 |
| 15 | 53.48 | 79.99 | 54.01 | 20.96 | 52.11 | 319.87 |
| 16 | 42.09 | 46.03 | 21.30 | 36.46 | 36.47 | 356.34 |
| 17 | | | 53.09 | 44.57 | 24.42 | 380.75 |
| 19 | 00.31 | | 50.81 | | 12.78 | 393.54 |
| Total: | 337.04 | 364.98 | 411.18 | 461.05 | | $S_{\bar{x}}$: 27.20 |

APPENDIX 2 (continued)

4. Fresh mass of foliage consumed per larva (mg) (continued)

4.4. *C. agricola - E. dalrympleana*

| | Replicate | | | | | |
|---|---|---|---|---|---|---|
| Day | 1 | 2 | 3 | 4 | Mean | Cumulative Mean |
| 1 | 1.77 | 0.57 | 1.20 | 1.66 | 1.30 | |
| 2 | 2.18 | | 2.34 | 2.79 | 1.83 | 3.13 |
| 4 | 1.12 | 0.64 | 1.38 | 5.80 | 0.78 | 3.91 |
| 5 | | | 4.58 | 11.44 | 2.59 | 6.51 |
| 7 | 5.62 | 3.79 | 3.93 | 11.47 | 6.19 | 12.70 |
| 8 | 5.05 | 8.86 | 12.10 | 10.04 | 9.37 | 22.07 |
| 9 | 28.55 | 10.13 | 12.36 | 44.27 | 8.85 | 30.92 |
| 10 | 10.89 | 18.95 | 51.89 | 26.90 | 31.50 | 62.42 |
| 11 | 14.78 | 21.77 | 20.27 | 30.17 | 20.93 | 83.34 |
| 12 | 14.21 | 13.12 | 26.62 | 47.88 | 21.03 | 104.37 |
| 13 | 30.13 | 44.81 | 37.62 | 55.82 | 40.11 | 144.49 |
| 14 | 35.99 | 45.93 | 49.87 | 47.14 | 46.90 | 191.39 |
| 15 | 50.84 | 55.09 | 48.61 | 65.10 | 50.42 | 241.81 |
| 16 | 41.60 | 46.20 | 47.13 | 31.35 | 50.01 | 291.81 |
| 17 | 60.39 | 43.21 | 45.99 | | 45.24 | 337.05 |
| 19 | 32.16 | | | | 8.04 | 345.09 |
| 20 | 0.32 | | 56.80 | | 14.28 | 359.37 |
| 21 | 32.27 | | 27.41 | | 14.92 | 374.29 |
| Total: | 367.87 | 313.07 | 450.10 | 391.83 | | $S_{\bar{x}}$: 28.40 |

APPENDIX 2 (continued)

5. Mean mass gain of larvae (mg)

5.1. *C. bimaculata* - *E. delegatensis*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 63.1 | 60.8 | 58.9 | 53.4 |
| | 58.7 | 64.4 | 55.6 | 62.5 |
| | 54.8 | 56.1 | 61.5 | 65.5 |
| | 53.3 | 57.6 | 60.6 | 57.7 |
| | 58.2 | 59.0 | 56.3 | 46.3 |
| | 48.1 | 48.0 | 50.6 | 58.7 |
| | 49.6 | 57.5 | 56.3 | 51.6 |
| | 48.6 | 50.6 | 69.2 | 50.3 |
| | 53.6 | 61.3 | 58.0 | 53.2 |
| | 52.7 | 46.8 | 59.7 | 63.0 |
| | 58.9 | 51.6 | 52.8 | 43.3 |
| | 57.2 | 60.9 | 49.5 | 47.4 |
| | 50.6 | 55.0 | 64.2 | 54.3 |
| | 58.2 | 55.3 | 60.9 | 52.8 |
| | 57.3 | 54.6 | 57.7 | 40.8 |
| | 53.3 | 50.3 | 53.0 | 54.9 |
| | 43.5 | 64.3 | 48.7 | 51.0 |
| | | 61.1 | 48.6 | 61.5 |
| | | 42.6 | 51.0 | 43.1 |
| | | 45.4 | 49.1 | 50.0 |
| | | 36.3 | | 56.5 |
| | | | | 50.9 |
| | | | | 48.1 |
| Mean prepupal mass:- | | | | |
| | 54.10 | 54.26 | 56.11 | 52.90 |
| Mean initial mass:- | | | | |
| | 0.06 | 0.06 | 0.06 | 0.06 |
| ∴ Mass gain:- | | | | |
| | 54.04 | 54.20 | 56.05 | 52.86 |

$\bar{x}^1$: 54.28 ± 0.66

5.2. *C. bimaculata* - *E. dalrympleana*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 60.9 | 59.0 | 57.8 | 59.6 |
| | 49.5 | 57.6 | 59.1 | 64.1 |
| | 49.8 | 48.3 | 53.0 | 71.4 |
| | 56.4 | 52.0 | 48.6 | 69.3 |
| | 60.6 | 54.6 | 62.4 | 60.7 |
| | 59.4 | 57.9 | 62.7 | 68.5 |
| | 55.4 | 41.8 | 54.0 | 59.9 |
| | 55.6 | 53.8 | 46.1 | 62.0 |
| | 49.2 | 43.8 | 63.2 | 56.7 |
| | 64.0 | 40.2 | 48.3 | 50.3 |
| | 59.8 | | | 55.3 |
| | 54.5 | | | 68.1 |
| | 53.5 | | | 60.0 |
| Mean prepupal mass:- | | | | |
| | 56.05 | 50.90 | 55.52 | 61.99 |
| Mean initial mass:- | | | | |
| | 0.06 | 0.06 | 0.06 | 0.07 |
| ∴Mass gain:- | | | | |
| | 55.59 | 50.84 | 55.46 | 61.92 |

$\bar{x}^1$: 55.95 ± 2.28

APPENDIX 2 (continued)

5. Mean mass gain of larvae (mg) (continued)

5.3. *C. agricola* - *E. delegatensis*

| Day | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 58.7 | 78.0 | 70.9 | 65.8 |
| | 65.2 | 71.5 | 52.0 | 65.9 |
| | 48.4 | 60.6 | 65.5 | 59.9 |
| | 53.2 | 52.2 | 54.2 | 62.6 |
| | 57.5 | 62.0 | 52.3 | 63.0 |
| | 51.6 | 54.1 | 56.9 | 70.4 |
| | 56.8 | 61.4 | 52.8 | 60.9 |
| | 65.2 | 52.6 | 64.1 | 60.8 |
| | 57.3 | 53.7 | 60.0 | 70.4 |
| | 48.0 | 61.9 | 61.1 | 68.8 |
| | | 65.9 | 54.6 | 64.0 |
| | | 54.3 | 59.9 | 62.7 |
| | | 51.7 | 58.6 | 62.4 |
| | | 61.2 | 38.0 | 51.4 |
| | | 50.3 | 53.9 | 67.8 |
| | | 50.5 | | 47.8 |
| | | 27.3 | | 73.7 |
| | | | | 57.9 |
| | | | | 56.7 |
| | | | | 55.5 |
| | | | | 70.3 |
| | | | | 47.4 |
| Mean prepupal mass:- | | | | |
| | 56.19 | 57.01 | 56.99 | 62.10 |
| Mean initial mass:- | | | | |
| | 0.04 | 0.05 | 0.05 | 0.05 |
| ∴ Mass gain:- | | | | |
| | 56.15 | 56.96 | 56.94 | 62.05 |

$\bar{x}^1$: 58.03 ± 1.35

5.4. *C. agricola* - *E. dalrympleana*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 59.4 | 65.6 | 59.9 | 71.4 |
| | 67.0 | 65.4 | 63.3 | 64.9 |
| | 67.4 | 58.4 | 56.1 | 64.3 |
| | 59.9 | 65.0 | 72.1 | 60.0 |
| | 68.5 | 69.6 | 54.3 | 69.5 |
| | 77.4 | 69.2 | 61.9 | 73.4 |
| | 61.0 | 64.5 | 64.1 | 52.5 |
| | 60.7 | 66.0 | 59.1 | 82.9 |
| | 59.6 | 55.3 | 61.5 | 52.6 |
| | 65.4 | 59.7 | 64.7 | 69.8 |
| | 65.1 | 68.0 | 59.7 | 64.7 |
| | 67.6 | 65.0 | 59.1 | 65.2 |
| | 59.5 | 56.7 | 62.6 | 63.0 |
| | 61.5 | 64.3 | 54.1 | 70.0 |
| | 57.4 | 58.0 | 44.3 | 65.6 |
| | 60.4 | 59.0 | 67.3 | 75.4 |
| | 56.2 | 76.1 | 48.5 | 62.0 |
| | 63.3 | 70.8 | 52.4 | 66.0 |
| | | 41.5 | 57.8 | 63.4 |
| | | | 51.9 | 62.1 |
| | | | | 67.5 |
| | | | | 69.4 |
| Mean prepupal mass:- | | | | |
| | 63.18 | 63.06 | 58.74 | 66.16 |
| Mean initial mass:- | | | | |
| | 0.05 | 0.05 | 0.05 | 0.05 |
| ∴ Mass gain:- | | | | |
| | 63.13 | 63.01 | 58.69 | 66.11 |

$\bar{x}^1$: 64.74 ± 1.53

APPENDIX 3

Larval feeding trial 2: Survival and growth rate of larvae of *C. bimaculata* and *C. agricola* on two *Monocalyptus* hosts (*E. delegatensis* and *E. regnans*) and two *Symphyomyrtus* hosts (*E. viminalis* and *E. globulus*).

1. Duration of larval feeding stage (days)

1.1. *C. bimaculata* - *E. delegatensis*

| duration | frequency |
|---|---|
| 12 | 31 |
| 13 | 15 |
| 14 | 5 |

1.2. *C. bimaculata* - *E. regnans*

| duration | frequency |
|---|---|
| 12 | 27 |
| 13 | 24 |
| 14 | 7 |
| 15 | 7 |
| 16 | 1 |

1.3. *C. bimaculata* - *E. viminalis*

| duration | frequency |
|---|---|
| 15 | 2 |
| 16 | 3 |
| 17 | 6 |
| 18 | 8 |
| 19 | 3 |

1.4. *C. bimaculata* - *E. globulus*

| duration | frequency |
|---|---|
| 16 | 3 |
| 17 | 3 |
| 18 | 1 |
| 20 | 2 |
| 22 | 5 |
| 23 | 2 |
| 24 | 1 |

APPENDIX 3 (continued)

1. Duration of larval feeding stage (days) (continued)

1.5. *C. agricola* - *E. delegatensis*

| duration | frequency |
|---|---|
| 14 | 43 |
| 15 | 19 |
| 16 | 8 |
| 17 | 4 |

1.6. *C. agricola* - *E. regnans*

| duration | frequency |
|---|---|
| 27 | 3 |
| 28 | 1 |
| 29 | 1 |
| 30 | 4 |
| 31 | 5 |

1.7. *C. agricola* - *E. viminalis*

| duration | frequency |
|---|---|
| 15 | 14 |
| 16 | 23 |
| 17 | 12 |
| 18 | 4 |
| 19 | 3 |
| 20 | 11 |
| 21 | 1 |
| 22 | 1 |

1.8. *C. agricola* - *E. globulus*

| duration | frequency |
|---|---|
| 14 | 2 |
| 15 | 13 |
| 16 | 18 |
| 17 | 14 |
| 18 | 8 |
| 19 | 1 |

APPENDIX 4

Laboratory feeding trial 3: Survival and growth rate of *C. bimaculata* larvae on *Monocalyptus* hosts of the series Obliquae (*E. obliqua, E. delegatensis, E. regnans* and *E. fastigata*) and the series Piperitae (*E. nitida*).

1. Survival until pupal stage:

Each replicate culture initially contained 25 larvae.

| | Replicates | | | | Total |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | |
| *E. obliqua* | 14 | 21 | 19 | 11 | 65 |
| *E. delegatensis* | 19 | 23 | 17 | 13 | 72 |
| *E. regnans* | 15 | 16 | 12 | 12 | 55 |
| *E. fastigata* | 15 | 22 | 23 | 18 | 78 |
| *E. nitida* | 12 | 6 | 11 | 9 | 38 |

APPENDIX 4 (continued)

2. Duration of larval-prepupal stage (days)

2.1. *E. obliqua*

| Rep. 1 | 2 | 3 | 4 |
|---|---|---|---|
| 12 | 12 | 12 | 12 |
| 12 | 12 | 12 | 13 |
| 12 | 12 | 12 | 14 |
| 12 | 12 | 12 | 14 |
| 13 | 12 | 12 | 14 |
| 13 | 12 | 12 | 14 |
| 13 | 13 | 12 | 14 |
| 13 | 13 | 13 | 15 |
| 14 | 13 | 13 | 15 |
| 15 | 13 | 13 | 15 |
| 16 | 14 | 13 | 16 |
| 16 | 14 | 13 | |
| 17 | 14 | 14 | |
| 18 | 14 | 14 | |
| | 14 | 14 | |
| | 14 | 14 | |
| | 15 | 14 | |
| | 16 | 15 | |
| | 15 | 15 | |
| | 15 | | |
| | 16 | | |
| $\bar{x}$ 14.00 | 13.52 | 13.11 | 14.18 |
| $\bar{x}^{-1}$: | 13.70 | | |
| $S_{\bar{x}}^{-1}$: | 0.24 | | |

2.2. *E. delegatensis*

| Rep. 1 | 2 | 3 | 4 |
|---|---|---|---|
| 12 | 11 | 12 | 11 |
| 12 | 11 | 12 | 12 |
| 12 | 11 | 12 | 12 |
| 12 | 11 | 12 | 12 |
| 12 | 11 | 12 | 12 |
| 12 | 11 | 12 | 13 |
| 12 | 12 | 12 | 13 |
| 12 | 12 | 12 | 13 |
| 13 | 12 | 12 | 13 |
| 13 | 12 | 12 | 13 |
| 13 | 12 | 12 | 13 |
| 13 | 12 | 12 | 13 |
| 13 | 12 | 12 | 14 |
| 13 | 12 | 12 | |
| 13 | 12 | 13 | |
| 13 | 13 | 13 | |
| 13 | 13 | 13 | |
| 15 | 13 | | |
| 15 | 13 | | |
| | 13 | | |
| | 13 | | |
| | 13 | | |
| | 16 | | |
| $\bar{x}$: 12.79 | 12.22 | 12.18 | 12.62 |
| $\bar{x}^{-1}$: | 12.45 | | |
| $S_{\bar{x}}^{-1}$: | 0.15 | | |

APPENDIX 4 (continued)

2. Duration of larval-prepupal stage (days) (continued)

2.3. *E. regnans*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 12 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 13 | 13 |
| | 13 | 13 | 14 | 14 |
| | 13 | 13 | 14 | 14 |
| | 14 | 13 | 14 | 14 |
| | 14 | 13 | 14 | 15 |
| | 15 | 14 | 16 | 15 |
| | 15 | 15 | | |
| | 16 | 15 | | |
| | 16 | 16 | | |
| | | 17 | | |
| $\bar{x}$: | 13.73 | 13.56 | 13.33 | 13.33 |
| $\bar{x}^{-1}$: | | 13.49 | | |
| $S_{\bar{x}}^{-1}$: | | 0.10 | | |

2.4. *E. fastigata*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 12 | 12 | 11 | 12 |
| | 12 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 12 | 12 | 12 |
| | 13 | 13 | 12 | 12 |
| | 13 | 13 | 12 | 12 |
| | 13 | 13 | 12 | 12 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 12 | 13 |
| | 13 | 13 | 12 | 13 |
| | 13 | 14 | 12 | 13 |
| | 14 | 15 | 12 | 13 |
| | 15 | 15 | 12 | 13 |
| | 15 | | 13 | 13 |
| | 15 | | 13 | 13 |
| | 16 | | 13 | 13 |
| | | | 13 | 14 |
| | | | 13 | 14 |
| | | | 14 | 14 |
| | | | 14 | 14 |
| | | | | 15 |
| $\bar{x}$: | 13.44 | 13.07 | 12.36 | 12.96 |
| $\bar{x}^{-1}$: | | 12.96 | | |
| $S_{\bar{x}}^{-1}$: | | 0.22 | | |

APPENDIX 4 (continued)

2. Duration of larval-prepupal stage (days) (continued)

2.5. *E. nitida*

| Rep. | 1 | 2 | 3 | 4 |
|---|---|---|---|---|
| | 13 | 15 | 15 | 14 |
| | 14 | 16 | 15 | 14 |
| | 14 | 16 | 15 | 15 |
| | 14 | 16 | 15 | 17 |
| | 15 | 18 | 17 | 17 |
| | 15 | 19 | 17 | 17 |
| | 15 | | 17 | 18 |
| | 15 | | 18 | 19 |
| | 15 | | 18 | 20 |
| | 16 | | 20 | |
| | 16 | | 21 | |
| | 16 | | | |
| $\bar{x}$: | 14.83 | 16.67 | 17.09 | 16.78 |

$\bar{x}^1$: 16.34

$S\bar{x}^1$: 0.51

APPENDIX 5

Estimation of numbers of shoots required for estimates of mean shoot occupancy and mean numbers per occupied shoot with 10% standard errors.

The estimates were based on sampling data of peak numbers recorded for each stage at Bunkers Thinned and Bunkers Grass in the 1973/74 season.

The shoot occupancy data fitted a binomial distribution of the form $(p + q)^n$ where:

p = mean presence = $\bar{x}$

q = mean absence = (1 - p)

n = number of shoots samples (= 60)

Standard error $(S_{\bar{x}}) = \sqrt{\frac{pq}{n}}$

The number of shoots required for a standard error of 10% of the mean shoot occupancy and of the mean numbers per occupied shoot was indicated by $n_{10\%}$.

APPENDIX 5

| | present/absence data | | | | numbers on occupied shoots | | | |
|---|---|---|---|---|---|---|---|---|
| | n | $\bar{x}(p)$ | $\frac{S\bar{x}}{\bar{x}} \times 100$ | $n_{10}\%$ | n | $\bar{x}$ | $\frac{S\bar{x}}{\bar{x}} \times 100$ | $n_{10}\%$ |
| Bunkers Thinned | | | | | | | | |
| Eggs 7.xii.73 | 60 | 0.467 | 13.8% | 114 | 28 | 31.96 | 12.8% | 46 |
| L1 12.xii.73 | 60 | 0.350 | 17.6% | 186 | 21 | 23.48 | 15.4% | 49 |
| L2-3 19.xii.73 | 60 | 0.417 | 15.3% | 139 | 25 | 16.28 | 21.4% | 115 |
| L4 24.xii.73 | 60 | 0.167 | 28.8% | 498 | 10 | 5.70 | 19.1% | 36 |
| Bunkers Grass | | | | | | | | |
| Eggs 14.xii.73 | 60 | 0.650 | 9.5% | 54 | 39 | 54.26 | 12.5% | 61 |
| L1 19.xii.73 | 60 | 0.300 | 19.7% | 233 | 18 | 30.89 | 19.2% | 66 |
| L2-3 28.xii.73 | 60 | 0.250 | 22.4% | 300 | 8 | 16.63 | 37.5% | 112 |
| L4 7.i.74 | 60 | 0.100 | 38.7% | 900 | 7 | 5.57 | 39.9% | 112 |

APPENDIX 6

Estimation of numbers of shoots per square metre at East Ridgley study site, 1975/76 season.

| Tree at sampling point: | Ratio of shoots early : late | Total shoots per tree late in season: |
|---|---|---|
| 1a | 5:9 | 262 |
| 1f | 5:6 | 285 |
| 2b | 5:8 | 211 |
| 2g | 5:7 | 322 |
| 3c | 5:7 | 304 |
| 3h | 5:9 | 189 |
| 4d | 5:10 | 335 |
| 4i | 5:14 | 554 |
| 5e | 5:7 | 664 |
| 5j | 5:11 | 390 |
| 6a | 5:5 | 297 |
| 6f | 5:8 | 478 |
| 7b | 5:8 | 355 |
| 7g | 5:8 | 772 |
| 8c | 5:9 | 313 |
| 8h | 5:9 | 116 |
| 9d | 5:10 | 698 |
| 9i | 5:7 | 288 |
| 10e | 5:6 | 568 |
| 10j | 5:7 | 157 |

APPENDIX 6

Summed ratio of shoots (20 trees) = 100 early : 165 late

Mean number of shoots per tree, late in season = 377.9±41.4 shoots

$\therefore$ mean number of shoots per tree, early in season = $\frac{377.9 \times 100}{165}$ shoots

= 229.0 shoots

$\therefore$ mean number of shoots per tree, mid season = $\frac{377.9 + 229.0}{2}$ shoots

= 303.4 shoots

Total area of study area = 37 m x 80 m

= 2960 $m^2$

$\therefore$ total trees in study area = 267 trees

$\therefore$ mean trees per square metre = $\frac{267}{2960}$

= .0902 trees.$m^{-2}$

$\therefore$ mean shoots per square metre = .0902 x 303.4 shoots.$m^{-2}$

= 27.36 shoots.$m^{-2}$

APPENDIX 7

Temperature-developmental data for eggs and larvae.

1. Eggs (after Greaves (1966))

| Temperature ($^{o}$F) : | 46 | 59 | 68 | 75 | 81 |
|---|---|---|---|---|---|
| ($^{o}$C) : | 8 | 15 | 20 | 24 | 27 |
| Incubation period (days): | 12.8 | 9.0 | 5.8 | 5.0 | 4.0 |

2. Larvae (after Greaves (unpublished information))

Constant temperature environments with a 16 hour photophase were maintained at temperatures of 8$^{o}$C, 15$^{o}$C, 20$^{o}$C, 24$^{o}$C, and 27$^{o}$C. Five replicate cultures were maintained at each temperature, each consisting of larvae from one egg batch. At the commencement of the trial, egg batches at the point of eclosion were selected and individually placed in petri dishes on fresh *E. regnans* foliage. Foliage was replaced at 24 hour intervals and numbers of larvae in each instar counted. The duration of an instar was estimated as the time from the point at which at least 50% of the surviving larvae entered that instar until the point at which at least 50% of the surviving larvae had entered the next instar. For the fourth instar larvae, only the duration of the active feeding period was measured.

APPENDIX 7 (continued)

| Temperature ($^{o}C$) : | | 8 | 15 | 20 | 24 | 27 |
|---|---|---|---|---|---|---|
| Incubation period (days) | | | | | | |
| of L1 | : | 11.4 | 6.4 | 4.0 | 3.0 | 2.0 |
| L2 | : | 9.2 | 5.2 | 2.8 | 1.8 | 2.0 |
| L1-2 | : | 20.6 | 11.6 | 6.8 | 4.8 | 4.0 |
| L3 | : | 9.6 | 5.0 | 2.4 | 2.4 | 2.0 |
| L4 (feeding stage) | : | 14.6 | 5.4 | 4.8 | 2.8 | 2.8 |

APPENDIX 8

Sampling data for eggs and larvae at Bunkers Thinned and Bunkers Grass study sites, 1973/74 season.

Sixty fixed tagged shoots were samples on ten trees (6 shoots per tree) for eggs and larvae.

Shoots were tagged on 12.xi.73 and re-tagged 18.i.74.

a = total nos. counted

b = estimated nos. per shoot

c = percentage shoot occupancy

APPENDIX 8 (continued)

1. Bunkers Thinned

| Date | Day | Eggs | | | L1 | | L2-3 | | L4 | | L1-4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | a | b | c | a | b | a | b | a | b | c |
| 15.xi.73 | 1 | 55 | 0.9 | 3 | | | | | | | |
| 20.xi.73 | 6 | 72 | 1.2 | 12 | | | | | | | |
| 26.xi.73 | 12 | 106 | 1.8 | 12 | | | | | | | |
| 29.xi.73 | 15 | 258 | 4.3 | 18 | 2 | | 6 | 0.1 | | | 2 |
| 4.xii.73 | 20 | 887 | 14.8 | 43 | 11 | 0.2 | 47 | 0.8 | | | 5 |
| 7.xii.73 | 23 | 895 | 14.9 | 47 | 6 | 0.1 | 188 | 3.1 | | | 2 |
| 10.xii.73 | 26 | 890 | 14.8 | 47 | 101 | 1.7 | 363 | 6.1 | | | 10 |
| 12.xii.73 | 28 | 342 | 5.7 | 27 | 546 | 9.1 | 204 | 3.4 | | | 40 |
| 14.xii.73 | 30 | 221 | 3.7 | 18 | 426 | 7.1 | 74 | 1.2 | | | 48 |
| 19.xii.73 | 35 | 36 | 0.6 | 3 | 74 | 1.2 | 28 | 0.5 | 10 | 0.2 | 50 |
| 23.xii.73 | 39 | 19 | 0.3 | 2 | 1 | | 9 | 0.2 | 42 | 0.7 | 33 |
| 24.xii.73 | 40 | 12 | 0.2 | 2 | | | 7 | 0.1 | 62 | 1.0 | 30 |
| 28.xii.73 | 44 | 1 | | 2 | | | | | 29 | 0.5 | 33 |
| 31.xii.73 | 47 | | | | | | | | 17 | 0.3 | 15 |

APPENDIX 8 (continued)

1. Bunkers Thinned (continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 3.i.74 | 53 | 26 | 0.4 | 2 | | | | | 1 | | 2 |
| 7.i.74 | 57 | 26 | 0.4 | 2 | | | | | 1 | | 2 |
| 10.i.74 | 60 | 41 | 0.7 | 3 | 21 | 0.4 | | | 3 | 0.1 | 7 |
| 14.i.74 | 64 | 209 | 3.5 | 13 | | | 2 | | | | 2 |
| 18.i.74 | 68 | 106 | 1.8 | 8 | | | | | | | |
| | shoots re-tagged | | | | | | | | | | |
| 21.i.74 | 71 | 427 | 7.1 | 23 | 231 | 3.9 | 10 | 0.2 | 2 | | 22 |
| 25.i.74 | 75 | 378 | 6.3 | 23 | 243 | 4.1 | 36 | 0.6 | | | 22 |
| 28.i.74 | 78 | 72 | 1.2 | 8 | 186 | 3.1 | 158 | 2.6 | | | 28 |
| 31.i.74 | 81 | | | | 31 | 0.5 | 141 | 2.4 | 30 | 0.5 | 27 |
| 4.ii.74 | 85 | | | | | | 26 | 0.4 | 10 | 0.2 | 15 |
| 7.ii.74 | 88 | | | | | | 8 | 0.1 | 1 | | 8 |
| 11.ii.74 | 92 | | | | | | 7 | 0.1 | 2 | | 10 |
| 15.ii.74 | 96 | | | | | | 3 | 0.1 | 3 | 0.1 | 7 |
| 20.ii.74 | 101 | | | | | | | | | | |

APPENDIX 8 (continued)

2. Bunkers Grass

| Date | Day | Eggs | | | L1 | | L2-3 | | L4 | | L1-4 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | a | b | c | a | b | a | b | a | b | c |
| 15.xi.73 | 1 | | | | | | | | | | |
| 20.xi.73 | 6 | | | | | | | | | | |
| 26.xi.73 | 12 | 19 | 0.3 | 2 | | | | | | | |
| 29.xi.73 | 15 | 38 | 0.6 | 2 | | | | | | | 2 |
| 4.xii.73 | 20 | 49 | 0.8 | 5 | | | | | | | |
| 7.xii.73 | 23 | 57 | 1.0 | 5 | | | | | | | |
| 19.xii.73 | 26 | 128 | 2.1 | 15 | | | | | | | |
| 12.xii.73 | 28 | 1834 | 30.6 | 60 | 10 | 0.2 | | | | | 2 |
| 14.xii.73 | 30 | 2124 | 35.4 | 65 | 14 | 0.2 | | | | | 3 |
| 19.xii.73 | 35 | 1341 | 22.4 | 58 | 538 | 9.0 | 6 | 0.1 | | | 32 |
| 23.xii.73 | 39 | 95 | 1.6 | 12 | 471 | 7.9 | 49 | 0.8 | 3 | 0.1 | 45 |
| 24.xii.73 | 40 | 59 | 1.0 | 8 | 294 | 4.9 | 129 | 2.2 | 3 | 0.1 | 45 |
| 28.xii.73 | 44 | 26 | 0.4 | 7 | 35 | 0.6 | 230 | 3.8 | 2 | | 33 |
| 31.xii.73 | 47 | 38 | 0.6 | 3 | 21 | 0.4 | 100 | 1.7 | 2 | | 30 |
| 3.i.74 | 53 | 84 | 1.4 | 7 | | | 118 | 2.0 | 2 | | 32 |

APPENDIX 8 (continued)

2. Bunkers Grass (continued)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 7.i.74 | 57 | 100 | 1.7 | 5 | | | 52 | 0.9 | 39 | 0.7 | 28 |
| 10.i.74 | 60 | 137 | 2.3 | 8 | | | 13 | 0.2 | 26 | 0.4 | 23 |
| 14.i.74 | 64 | 142 | 2.4 | 8 | 43 | 0.7 | | | | | 7 |
| 18.i.74 | 68 | 170 | 2.8 | 8 | 54 | 0.9 | 25 | 0.4 | | | 7 |
| | shoots re-tagged | | | | | | | | | | |
| 21.i.74 | 71 | 56 | 1.0 | 5 | 23 | 0.4 | 104 | 1.7 | | | 18 |
| 25.i.74 | 75 | 32 | 0.5 | 3 | 17 | 0.3 | 67 | 1.1 | 1 | | 15 |
| 28.i.74 | 78 | | | | 9 | 0.2 | 19 | 0.3 | 16 | 0.3 | 22 |
| 31.i.74 | 81 | | | | 5 | 0.1 | | | 14 | 0.2 | 12 |
| 4.ii.74 | 85 | | | | | | | | | | |
| 7.ii.74 | 88 | | | | | | | | | | |
| 11.ii.74 | 92 | | | | | | | | | | |
| 15.ii.74 | 96 | 56 | 1.0 | 3 | | | | | | | |
| 20.ii.74 | 101 | 30 | 0.5 | 2 | | | | | | | 2 |

APPENDIX 9

Shoot occupancy data for eggs and larvae at Bunkers Thinned study site, 1974/75 season, and at East Ridgley study site, 1974/75 and 1975/76 seasons. (Destructive sampling technique)

T.S.S. = total shoots sampled on sampling date

S.O. = shoots occupied

% S.O. = % of shoots occupied

S.E. % = mean occupancy standard error as % of mean

O.S.[1] = occupied shoots sub-sampled for numbers data

APPENDIX 9 (continued)

1. Bunkers Thinned, 1974/75

| Date | Day | T.S.S. | Stage | S.O. | % S.O. | S.E. % | O.S.[1] |
|---|---|---|---|---|---|---|---|
| 12.xii.74 | 1 | 500 | | | | | |
| 20.vii.74 | 9 | 395 | E | 19 | 5 | 22 | 19 |
| | | | L1 | 1 | | | |
| 29.xii.74 | 16 | 448 | E | 21 | 5 | 21 | 21 |
| 3.i.75 | 23 | 369 | E | 56 | 15 | 12 | 49 |
| | | | L1 | 3 | 1 | | 3 |
| 11.i.75 | 31 | 354 | E | 37 | 10 | 16 | 34 |
| | | | L1 | 16 | 5 | 24 | 15 |
| | | | L2 | 2 | | | 2 |
| 18.i.75 | 38 | 336 | E | 31 | 9 | 17 | 25 |
| | | | L1 | 23 | 8 | | 18 |
| | | | L2 | 4 | | | 4 |
| 24.i.75 | 44 | 343 | E | 22 | 6 | 21 | 19 |
| | | | L1 | 19 | 11 | | 16 |
| | | | L2 | 18 | | | 17 |
| | | | L3 | 9 | | | 9 |
| | | | L4 | 1 | | | |
| 29.i.75 | 49 | 361 | E | 32 | 9 | 17 | 29 |
| | | | L1 | 13 | 7 | | 13 |
| | | | L2 | 14 | | | 14 |
| | | | L3 | 8 | | | 7 |
| | | | L4 | 1 | | | 1 |

APPENDIX 9 (continued)

1. Bunkers Thinned, 1974/75 (continued)

| Date | Day | T.S.S. | Stage | S.O. | % S.O. | S.E. % | O.S.[1] |
|---|---|---|---|---|---|---|---|
| 4.ii.75 | 55 | 363 | E | 25 | 7 | 19 | 25 |
| | | | L1 | 17 | 8 | | 16 |
| | | | L2 | 9 | | | 9 |
| | | | L3 | 11 | | | 11 |
| | | | L4 | 2 | | | 2 |
| 8.ii.75 | 59 | 298 | E | 48 | 16 | 13 | 39 |
| | | | L1 | 5 | 10 | | 4 |
| | | | L2 | 16 | | | 8 |
| | | | L3 | 15 | | | 10 |
| | | | L4 | 7 | | | 6 |
| 13.ii.75 | 64 | 287 | E | 40 | 14 | 15 | 33 |
| | | | L1 | 17 | 15 | 20 | 15 |
| | | | L2 | 8 | | | 7 |
| | | | L3 | 18 | | | 15 |
| | | | L4 | 11 | | | 7 |
| 20.ii.75 | 71 | 325 | E | 17 | 5 | 24 | 16 |
| | | | L1 | 23 | 17 | | 20 |
| | | | L2 | 16 | | | 12 |
| | | | L3 | 5 | | | 5 |
| | | | L4 | 16 | | | 14 |
| 25.ii.75 | 76 | 286 | E | 12 | 4 | 28 | 12 |
| | | | L1 | 8 | 18 | 17 | 7 |
| | | | L2 | 21 | | | 27 |
| | | | L3 | 11 | | | 11 |
| | | | L4 | 12 | | | 11 |

APPENDIX 9 (continued)

1. Bunkers Thinned, 1974/75 (continued)

| Date | Day | T.S.S. | Stage | S.O. | % S.O. | S.E. % | O.S.[1] |
|---|---|---|---|---|---|---|---|
| 3.iii.75 | 82 | 234 | E | 3 | 1 | 57 | 3 |
| | | | L1 | 3 | 31 | | 2 |
| | | | L2 | 19 | | | 16 |
| | | | L3 | 46 | | 13 | 34 |
| | | | L4 | 27 | | | 20 |
| 10.iii.75 | 89 | 311 | L1 | 2 | 21 | | 2 |
| | | | L2 | 16 | | | 14 |
| | | | L3 | 19 | | | 18 |
| | | | L4 | 43 | | 14 | 38 |
| 20.iii.75 | 99 | 441 | L2 | 3 | 8 | | 2 |
| | | | L3 | 20 | | | 19 |
| | | | L4 | 16 | | | 16 |
| 25.iii.75 | 104 | 500 | L3 | 1 | | | 1 |
| | | | L4 | 1 | | | 1 |

APPENDIX 9 (continued)

2. East Ridgley, 1974/75

| Date | T.S.S. | Stage | S.O. | % S.O. | S.E. % | O.S.[1] |
|---|---|---|---|---|---|---|
| 22.xii.74 | 389 | E | 49 | 13 | 13 | 37 |
| 1.i.75 | 322 | E | 62 | 19 | 11 | 49 |
| 10.i.75 | 354 | E | 16 | 5 | | 15 |
| | | L1 | 27 | 14 | 18 | 22 |
| | | L2 | 34 | | 16 | 24 |
| 17.i.75 | 240 | E | 10 | 4 | | 8 |
| | | L1 | 23 | | 20 | 18 |
| | | L2 | 34 | 28 | 16 | 24 |
| | | L3 | 48 | | 13 | 39 |
| 22.i.75 | 283 | L2 | 23 | | | 17 |
| | | L3 | 31 | 22 | | 23 |
| | | L4 | 43 | | | 35 |
| 27.i.75 | 278 | E | 1 | | | 1 |
| | | L2 | 3 | | | 3 |
| | | L3 | 13 | 17 | | 11 |
| | | L4 | 38 | | 15 | 33 |
| 3.ii.75 | 500 | E | 2 | | | 2 |
| | | L1 | 1 | | | 1 |
| | | L2 | 1 | | | 1 |
| | | L3 | 2 | 2 | | 2 |
| | | L4 | 4 | | | 4 |
| 10.ii.75 | 484 | E | 3 | 1 | | 3 |
| | | L1 | 4 | | | 4 |
| | | L2 | 5 | 2 | | 5 |
| | | L3 | 1 | | | 1 |
| | | L4 | 1 | | | 1 |

APPENDIX 9 (continued)

2. East Ridgley, 1974/75 (continued)

| Date | T.S.S. | Stage | S.O. | % S.O. | S.E. % | O.S.[1] |
|---|---|---|---|---|---|---|
| 18.ii.75 | 471 | E | 9 | 2 | | 9 |
| | | L1 | 2 | | | 2 |
| | | L2 | 6 | 3 | | 6 |
| | | L3 | 4 | | | 4 |
| 24.ii.75 | 478 | E | 2 | 1 | | 2 |
| | | L1 | 5 | | | 5 |
| | | L2 | 3 | 2 | | 3 |
| | | L3 | 5 | | | 5 |
| | | L4 | 2 | | | 2 |
| 5.iii.75 | 452 | E | 3 | 1 | | 3 |
| | | L1 | 5 | | | 5 |
| | | L2 | 5 | 5 | | 5 |
| | | L3 | 8 | | | 8 |
| | | L4 | 8 | | | 8 |
| 14.iii.75 | 475 | L1 | 3 | | | 3 |
| | | L2 | 2 | 7 | | 2 |
| | | L3 | 6 | | | 6 |
| | | L4 | 3 | | | 3 |

APPENDIX 9 (continued)

3. East Ridgley, 1975/76

| Date | Stage | T.S.S. | S.O. | % S.O. | S.E. % | O.S.[1] |
|---|---|---|---|---|---|---|
| 13.xi.75 | E | 500 | 1 | | | 1 |
| 21.xi.75 | E | 462 | 23 | 5 | 20 | 23 |
| 27.xi .75 | E | 293 | 77 | 26 | 10 | 54 |
| | L1-3 | 308 | 1 | | | 1 |
| 2.xii.75 | E | 235 | 87 | 37 | 9 | 60 |
| | L1-3 | 278 | 6 | 2 | 40 | 6 |
| 8.xii.75 | E | 483 | 12 | 2 | 24 | 12 |
| | L1-3 | 244 | 78 | 32 | 9 | 59 |
| 12.xii.75 | L1-3 | 241 | 86 | 36 | 9 | 60 |
| 18.xii.75 | L1-3 | 275 | 74 | 27 | 10 | 53 |
| | L4 | 391 | 37 | 9 | 16 | 33 |
| 22.xii.75 | L1-3 | 396 | 49 | 12 | 13 | 35 |
| | L4 | 306 | 66 | 22 | 11 | 44 |
| 26.xii.75 | L4 | 396 | 53 | 13 | 13 | 44 |
| 1.i.76 | E | 500 | 2 | | | |
| 9.i.76 | E | 500 | 3 | 1 | | |
| | L1-3 | 500 | 7 | 1 | | |
| 15.i.76 | E | 493 | 9 | 2 | | |
| | L1-3 | 489 | 7 | 1 | | |
| 22.i.76 | E | 500 | 3 | 1 | | |
| | L1-3 | 500 | 5 | 1 | | |
| | L4 | 500 | 1 | | | |

APPENDIX 9 (continued)

3. East Ridgley, 1975/76 (continued)

| Date | Stage | T.S.S. | S.O. | % S.O. |
|---|---|---|---|---|
| 29.i.76 | E | 500 | 6 | 1 |
| | L1-3 | 500 | 4 | 1 |
| | L4 | 485 | 3 | 1 |
| 5.ii.76 | E | 500 | 4 | 1 |
| | L1-3 | 500 | 3 | 1 |
| 13.ii.76 | E | 500 | 5 | 1 |
| | L1-3 | 500 | 5 | 1 |

APPENDIX 10

Numbers data for eggs and larvae at Bunkers Thinned study site, 1974/75 season, and at East Ridgley study site, 1974/75 and 1975/76 season.

T.B. = total egg batches

T.E. = total eggs

T.pr. = total eggs recorded predated

T.pa. = total eggs recorded parasitized

L1 = total first instar larvae

L2 = total second instar larvae

L1-2 = L1 + L2

L3 = total third instar larvae

L4 = total fourth instar larvae

T = total L4 parasitized by tachinid

B = total L4 parasitized by braconid

X = total L4 dying of unidentified cause in laboratory

APPENDIX 10 (continued)

1. Eggs

1.a. Bunkers Thinned, 1974/75. Eggs

a = no./0.S.; b = no./shoot

| | T.B. | | T.E. | | T.pr. | | T.pa. | |
|---|---|---|---|---|---|---|---|---|
| Day | a | b | a | b | a | b | a | b |
| 9 | 25 | 0.06 | 555 | 1.40 | 86 | 0.22 | 156 | 0.39 |
| 16 | 32 | 0.07 | 806 | 1.80 | 237 | 0.53 | | |
| 23 | 73 | 0.23 | 1871 | 5.80 | 514 | 1.59 | 160 | 0.49. |
| 31 | 41 | 0.13 | 1115 | 3.43 | 324 | 1.00 | 349 | 1.07 |
| 38 | 32 | 0.12 | 880 | 3.26 | 235 | 0.87 | 54 | 0.20 |
| 44 | 26 | 0.09 | 816 | 2.76 | 216 | 0.57 | 160 | 0.54 |
| 49 | 45 | 0.14 | 1264 | 3.86 | 257 | 0.79 | 240 | 0.73 |
| 55 | 29 | 0.08 | 824 | 2.27 | 204 | 0.56 | 342 | 0.94 |
| 59 | 68 | 0.28 | 1649 | 6.81 | 261 | 1.08 | 116 | 0.48 |
| 64 | 46 | 0.19 | 1180 | 4.98 | 293 | 1.24 | 163 | 0.69 |
| 71 | 18 | 0.06 | 368 | 1.20 | 81 | 0.27 | | |
| 76 | 16 | 0.06 | 287 | 1.00 | 59 | 0.21 | 171 | 0.60 |
| 82 | 5 | 0.02 | 81 | 0.34 | 52 | 0.22 | 11 | 0.05 |

APPENDIX 10 (continued)

1. Eggs (continued)

1.b. East Ridgley, 1974/75. Eggs

| | T.B. | | T.E. | | T.pr. | | T.pa. | |
|---|---|---|---|---|---|---|---|---|
| Day | a | b | a | b | a | b | a | b |
| 1 | 95 | 0.32 | 2368 | 8.04 | 202 | 0.69 | 51 | 0.17 |
| 11 | 85 | 0.33 | 2007 | 7.72 | 1133 | 4.37 | 170 | 0.86 |
| 20 | 20 | 0.06 | 552 | 1.71 | 188 | 0.58 | 163 | 0.51 |
| 27 | 10 | 0.05 | 304 | 1.58 | 1.18 | 0.61 | 143 | 0.74 |

1.c. East Ridgley, 1975/76. Eggs

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 1 | 1 | | 38 | 0.08 | | | | |
| 9 | 39 | 0.08 | 1084 | 2.35 | 74 | 0.16 | 23 | 0.05 |
| 15 | 117 | 0.57 | 3251 | 15.82 | 786 | 3.83 | 132 | 0.64 |
| 20 | 119 | 0.73 | 3412 | 21.05 | 1487 | 9.18 | 71 | 0.44 |
| 26 | 14 | 0.03 | 429 | 0.89 | 200 | 0.41 | 126 | 0.26 |

APPENDIX 10 (continued)

2. First to Third instar larvae

2.a. Bunkers Thinned, 1974/75

| | L1 | | L2 | | L1-2 | L3 | |
|---|---|---|---|---|---|---|---|
| Day | a | b | a | b | L1b + L2b | a | b |
| 23 | 28 | 0.08 | | | 0.08 | | |
| 31 | 200 | 0.60 | 10 | 0.03 | 0.63 | | |
| 38 | 270 | 1.30 | 36 | 0.11 | 1.14 | | |
| 44 | 187 | 0.65 | 202 | 0.62 | 1.27 | 43 | 0.13 |
| 49 | 178 | 0.46 | 131 | 0.36 | 0.82 | 3 | 0.04 |
| 55 | 244 | 0.71 | 90 | 0.25 | 0.96 | 43 | 0.12 |
| 59 | 24 | 0.10 | 165 | 1.11 | 1.21 | 49 | 0.16 |
| 64 | 189 | 0.75 | 66 | 0.26 | 1.01 | 75 | 0.32 |
| 71 | 193 | 0.68 | 175 | 0.72 | 1.40 | 25 | 0.08 |
| 76 | 82 | 0.33 | 359 | 1.44 | 1.77 | 118 | 0.41 |
| 82 | 15 | 0.10 | 16 | 0.60 | 0.70 | 229 | 1.32 |
| 89 | 2 | 0.01 | 66 | 0.24 | 0.25 | 90 | 0.31 |
| 99 | | | 2 | 0.01 | 0.01 | 62 | 0.15 |
| 104 | | | | | | 6 | 0.01 |

APPENDIX 10 (continued)

2. First to Third instar larvae (continued)

2.b. East Ridgley, 1974/75

| | L1 | | L2 | | L1-2 | L3 | |
|---|---|---|---|---|---|---|---|
| Day | a | b | a | b | L1b + L2b | a | b |
| 20 | 200 | 0.69 | 223 | 0.89 | 1.58 | | |
| 27 | 273 | 1.45 | 75 | 0.44 | 1.89 | 228 | 1.17 |
| 32 | | | 74 | 0.35 | 0.35 | 43 | 0.20 |
| 37 | | | 4 | 0.01 | 0.01 | 32 | 0.14 |
| 44 | | | | | | | |

2.c. East Ridgley, 1975/76

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 20 | 108 | 0.39 | | | 0.39 | | |
| 26 | 1318 | 7.14 | 262 | 1.42 | 8.56 | | |
| 30 | 132 | 0.79 | 881 | 5.24 | 6.03 | 157 | 0.93 |
| 36 | 9 | 0.05 | 37 | 0.19 | 0.24 | 388 | 1.97 |
| 40 | | | 9 | 0.03 | 0.03 | 129 | 0.46 |

APPENDIX 10 (continued)

3. Fourth Instar Larvae

3.a. Bunkers Thinned, 1974/75

| | L4 | | T | | B | | X | |
|---|---|---|---|---|---|---|---|---|
| Day | a | b | a | b | a | b | a | b |
| 44 | 1 | | 1 | | | | | |
| 49 | 2 | 0.01 | 2 | 0.01 | | | | |
| 55 | 3 | 0.01 | 2 | 0.01 | | | | |
| 59 | 9 | 0.04 | 2 | 0.02 | 4 | 0.01 | | |
| 64 | 16 | 0.09 | 5 | 0.03 | 2 | 0.01 | | |
| 71 | 38 | 0.13 | 13 | 0.05 | 2 | 0.01 | 2 | 0.01 |
| 76 | 18 | 0.07 | 8 | 0.03 | 1 | | 1 | |
| 82 | 41 | 0.24 | 20 | 0.12 | | | 2 | 0.01 |
| 89 | 84 | 0.31 | 37 | 0.14 | 1 | | 4 | 0.02 |
| 99 | 31 | 0.07 | 5 | 0.01 | | | | |
| 104 | 6 | 0.01 | 2 | | | | | |

APPENDIX 10 (continued)

3. Fourth Instar Larvae

3.b. East Ridgley, 1974/75

| | L4 | | T | | B | | X | |
|---|---|---|---|---|---|---|---|---|
| Day | a | b | a | b | a | b | a | b |
| 32 | 102 | 0.44 | 8 | 0.03 | 63 | 0.27 | 12 | 0.05 |
| 37 | 49 | 0.20 | 2 | 0.01 | 37 | 0.15 | 7 | 0.03 |
| 44 | 4 | 0.01 | | | 4 | 0.01 | | |

3.c. East Ridgley, 1974/75

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 36 | 78 | 0.22 | 7 | 0.02 | 24 | 0.07 | 12 | 0.03 |
| 40 | 210 | 1.03 | 16 | 0.08 | 74 | 0.36 | 6 | 0.03 |
| 44 | 134 | 0.41 | 14 | 0.04 | 47 | 0.14 | 3 | 0.01 |

APPENDIX 11

Maximum, minimum, and squared mean temperatures.

1. for Bunkers Thinned, December 1974 to March 1975 ($^{o}C$)

| | December | | | January | | | February | | | March | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 1 | 16 | 8 | | 15 | 5 | 11.2 | 25 | 8 | 18.6 | 17 | 9 | 13.6 |
| 2 | 12 | 5 | | 16 | 7 | 12.3 | 20 | 7 | 15.0 | 19 | 13 | 16.3 |
| 3 | 9 | 4 | | 18 | 5 | 13.2 | 18 | 8 | 13.9 | 16 | 10 | 13.3 |
| 4 | 11 | 5 | | 14 | 7 | 11.1 | 22 | 8 | 16.6 | 17 | 10 | 13.9 |
| 5 | 14 | 7 | | 17 | 7 | 13.0 | 20 | 10 | 15.8 | 24 | 8 | 17.9 |
| 6 | 15 | 6 | | 15 | 7 | 11.7 | 28 | 8 | 20.6 | 21 | 13 | 17.5 |
| 7 | 11 | 4 | | 17 | 7 | 13.0 | 32 | 13 | 24.4 | 19 | 11 | 15.5 |
| 8 | 17 | 6 | | 17 | 11 | 14.3 | 27 | 11 | 20.6 | 17 | 9 | 13.6 |
| 9 | 14 | 7 | | 12 | 7 | 9.8 | 20 | 11 | 18.1 | 18 | 9 | 14.2 |
| 10 | 11 | 5 | | 12 | 6 | 9.5 | 19 | 11 | 15.5 | 19 | 11 | 15.5 |
| 11 | 14 | 8 | | 10 | 4 | 7.6 | 22 | 9 | 16.8 | 18 | 12 | 15.3 |
| 12 | 14 | 6 | 10.8 | 12 | 5 | 9.2 | 13 | 7 | 10.4 | 17 | 11 | 14.3 |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

1. for Bunkers Thinned, December 1974 to March 1975 ($^{o}C$) (continued)

| | December | | | January | | | February | | | March | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 13 | 17 | 8 | 13.3 | 10 | 7 | 8.6 | 14 | 7 | 11.1 | 17 | 10 | 13.9 |
| 14 | 22 | 7 | 16.3 | 13 | 7 | 10.4 | 20 | 6 | 14.8 | 18 | 13 | 15.7 |
| 15 | 16 | 9 | 13.0 | 17 | 3 | 12.2 | 15 | 8 | 12.0 | 15 | 10 | 12.7 |
| 16 | 18 | 7 | 13.7 | 15 | 9 | 12.4 | 18 | 5 | 13.2 | 16 | 10 | 13.3 |
| 17 | 12 | 9 | 10.6 | 16 | 6 | 12.1 | 20 | 7 | 15.0 | 16 | 10 | 13.3 |
| 18 | 11 | 8 | 9.6 | 13 | 6 | 10.1 | 26 | 15 | 21.2 | 14 | 12 | 13.0 |
| 19 | 8 | 5 | 6.7 | 20 | 3 | 14.3 | 20 | 11 | 16.1 | 13 | 10 | 11.6 |
| 20 | 12 | 6 | 9.5 | 19 | 10 | 15.2 | 19 | 8 | 14.6 | 13 | 8 | 10.8 |
| 21 | 20 | 7 | 15.0 | 20 | 7 | 15.0 | 18 | 11 | 14.9 | 15 | 10 | 12.7 |
| 22 | 22 | 9 | 16.8 | 15 | 8 | 12.0 | 19 | 8 | 14.6 | 17 | 6 | 12.7 |
| 23 | 16 | 10 | 13.3 | 14 | 5 | 10.5 | 22 | 11 | 17.4 | 14 | 9 | 11.8 |
| 24 | 14 | 11 | 12.6 | 17 | 5 | 12.5 | 21 | 11 | 16.8 | 12 | 7 | 9.8 |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

1. for Bunkers Thinned, December 1974 to March 1975 ($^{o}C$) (continued)

| | December | | | January | | | February | | | March | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 25 | 13 | 6 | 10.1 | 15 | 8 | 12.0 | 19 | 10 | 15.2 | 12 | 7 | 9.8 |
| 26 | 13 | 4 | 9.6 | 10 | 7 | 8.6 | 20 | 10 | 15.8 | 18 | 8 | |
| 27 | 16 | 8 | 12.6 | 16 | 6 | 12.1 | 20 | 10 | 15.8 | 15 | 10 | |
| 28 | 11 | 9 | 10.0 | 16 | 6 | 12.1 | 19 | 6 | 14.1 | 14 | 9 | |
| 29 | 12 | 9 | 10.6 | 19 | 6 | 14.1 | | | | 13 | 7 | |
| 30 | 11 | 9 | 10.0 | 20 | 10 | 15.8 | | | | 12 | 6 | |
| 31 | 11 | 6 | 8.9 | 23 | 10 | 17.7 | | | | 10 | 5 | |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

2. East Ridgley, December 1974 to March 1975

| | December | | | January | | | February | | | March | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 1 | 24 | 12 | | 16 | 5 | 11.9 | 27 | 10 | 20.4 | 17 | 8 | 13.3 |
| 2 | 15 | 6 | | 20 | 10 | 15.8 | 24 | 11 | 18.7 | 20 | 14 | 17.3 |
| 3 | 13 | 4 | | 19 | 7 | 14.3 | 20 | 13 | 16.9 | 17 | 10 | 14.0 |
| 4 | 14 | 6 | | 17 | 9 | 13.6 | 27 | 10 | 20.4 | 20 | 9 | 15.5 |
| 5 | 19 | 7 | | 21 | 7 | 15.7 | 20 | 12 | 16.5 | 21 | 9 | 16.2 |
| 6 | 18 | 6 | | 17 | 9 | 13.6 | 26 | 11 | 20.0 | 20 | 13. | 16.9 |
| 7 | 15 | 5 | | 19 | 9 | 14.9 | 30 | 13 | 23.1 | 21 | 11 | 16.8 |
| 8 | 17 | 7 | | 21 | 14 | 17.9 | 28 | 12 | 21.5 | 18 | 11 | 14.9 |
| 9 | 14 | 10 | | 14 | 9 | 11.8 | 21 | 11 | 16.8 | 17 | 9 | 13.6 |
| 10 | 14 | 7 | | 13 | 6 | 10.1 | 22 | 11 | 17.4 | 19 | 10 | 15.2 |
| 11 | 14 | 8 | | 11 | 6 | 8.9 | 22 | 9 | 16.8 | 18 | 13 | 15.7 |
| 12 | 18 | 6 | | 15 | 6 | 11.4 | 15 | 8 | 12.0 | 17 | 10 | 14.0 |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

2. East Ridgley, December 1974 to March 1975 (continued)

| | December | | | January | | | February | | | March | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 13 | 21 | 10 | | 15 | 8 | 12.0 | 15 | 6 | 11.4 | 17 | 9 | 13.6 |
| 14 | 21 | 9 | | 18 | 8 | 13.9 | 22 | 8 | 16.6 | 17 | 13 | 15.1 |
| 15 | 18 | 11 | | 16 | 5 | 11.9 | 17 | 9 | 13.6 | 16 | 8 | 12.7 |
| 16 | 18 | 9 | | 13 | 11 | 12.0 | 18 | 9 | 14.2 | 16 | 8 | 12.7 |
| 17 | 17 | 8 | | 17 | 9 | 13.6 | 19 | 11 | 15.5 | 17 | 8 | 13.3 |
| 18 | 15 | 8 | | 16 | 8 | 12.7 | 23 | 12 | 18.3 | 14 | 12 | 13.0 |
| 19 | 11 | 7 | | 18 | 7 | 13.7 | 22 | 12 | 17.7 | 13 | 8 | 10.8 |
| 20 | 17 | 7 | | 19 | 11 | 15.5 | 19 | 9 | 14.9 | 14 | 7 | 11.1 |
| 21 | 25 | 8 | | 22 | 11 | 17.4 | 18 | 11 | 14.9 | 17 | 9 | 13.6 |
| 22 | 20 | 10 | 15.8 | 19 | 10 | 15.2 | 18 | 10 | 14.6 | 18 | 8 | 13.9 |
| 23 | 16 | 11 | 13.7 | 16 | 7 | 12.4 | 20 | 11 | 16.1 | 15 | 7 | 11.7 |
| 24 | 16 | 13 | 14.6 | 18 | 6 | 13.4 | 20 | 9 | 15.5 | 13 | 6 | 10.1 |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

2. East Ridgley, December 1974 to March 1975 (continued)

| | December | | | January | | | February | | | March | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 25 | 16 | 7 | 12.4 | 18 | 9 | 14.2 | 19 | 11 | 15.5 | 13 | 5 | 9.9 |
| 26 | 15 | 6 | 11.4 | 13 | 8 | 10.8 | 21 | 10 | 16.5 | 16 | 6 | 12.1 |
| 27 | 17 | 8 | 13.3 | 19 | 5 | 13.9 | 18 | 11 | 14.9 | 13 | 9 | 11.2 |
| 28 | 13 | 10 | 11.6 | 18 | 9 | 14.2 | 17 | 8 | 13.3 | 14 | 6 | 10.8 |
| 29 | 16 | 10 | 13.3 | 19 | 9 | 14.9 | | | | 13 | 7 | 10.4 |
| 30 | 15 | 8 | 12 | 20 | 11 | 16.1 | | | | 13 | 4 | 9.6 |
| 31 | 16 | 6 | 12.1 | 21 | 12 | 17.1 | | | | 10 | 3 | 7.4 |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

3. East Ridgley, November 1975 to February 1976

| | November | | | December | | | January | | | February | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 1 | 15 | 5 | | 20 | 10 | 15.8 | 21 | 10 | 16.5 | 20 | 9 | 15.5 |
| 2 | 10 | 6 | | 17 | 11 | 14.3 | 26 | 11 | 20 | 20 | 8 | |
| 3 | 10 | 6 | | 22 | 10 | 17.1 | 26 | 11 | 20 | 22 | 10 | |
| 4 | 11 | 8 | | 17 | 9 | 13.6 | 29 | 12 | 22.2 | 23 | 13 | |
| 5 | 17 | 8 | | 18 | 7 | 13.7 | 21 | 11 | 16.8 | 24 | 13 | |
| 6 | 15 | 8 | | 18 | 13 | 15.7 | 20 | 13 | 16.9 | 20 | 12 | |
| 8 | 14 | 6 | | 21 | 12 | 17.1 | 17 | 9 | 13.6 | 18 | 13 | |
| 9 | 18 | 8 | | 18 | 9 | 14.2 | 15 | 6 | 11.4 | 21 | 11 | |
| 10 | 17 | 10 | | 20 | 7 | 15.0 | 20 | 4 | 14.4 | 15 | 11 | |
| 11 | 18 | 10 | | 22 | 11 | 17.4 | 19 | 11 | 15.5 | 21 | 9 | |
| 12 | 21 | 9 | | 27 | 13 | 21.2 | 19 | 14 | 16.7 | 19 | 13 | |
| 13 | 17 | 10 | 14.0 | 19 | 10 | 15.2 | 22 | 15 | 18.8 | 20 | 14 | |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

3. East Ridgley, November 1975 to February 1976 (continued)

| | November | | | December | | | January | | | February | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 14 | 19 | 14 | 16.7 | 16 | 12 | 14.1 | 19 | 13 | 16.3 | 25 | 10 | |
| 15 | 23 | 12 | 18.3 | 21 | 11 | 16.8 | 19 | 11 | 15.5 | 21 | 9 | |
| 16 | 17 | 10 | 14.0 | 16 | 11 | 13.7 | 20 | 10 | 15.8 | 21 | 14 | |
| 17 | 15 | 9 | 12.4 | 15 | 9 | 12.4 | 21 | 10 | 16.4 | 18 | 14 | |
| 18 | 22 | 13 | 18.1 | 16 | 7 | 12.4 | 23 | 12 | 18.3 | 22 | 12 | |
| 19 | 17 | 14 | 15.6 | 16 | 6 | 12.1 | 20 | 15 | 17.7 | 19 | 16 | |
| 20 | 20 | 13 | 16.9 | 23 | 10 | 17.7 | 21 | 8 | 15.9 | 23 | 8 | |
| 21 | 25 | 13 | 19.9 | 21 | 11 | 16.8 | 21 | 15 | 18.2 | 22 | 11 | |
| 22 | 15 | 13 | 14.0 | 19 | 8 | 14.6 | 21 | 12 | 17.1 | 22 | 11 | |
| 23 | 15 | 8 | 12.0 | 20 | 9 | 15.5 | 15 | 11 | 13.2 | 25 | 15 | |
| 24 | 14 | 6 | 10.8 | 21 | 7 | 15.7 | 17 | 8 | 13.3 | 27 | 16 | |
| 25 | 13 | 6 | 10.1 | 18 | 7 | 13.7 | 17 | 8 | 13.3 | 25 | 17 | |

APPENDIX 11 (continued)

Maximum, minimum, and squared mean temperatures. (continued)

3. East Ridgley, November 1975 to December 1976 (continued)

| | November | | | December | | | January | | | February | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Date | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ | Max | Min | $\bar{x}^2$ |
| 26 | 14 | 6 | 10.8 | 18 | 11 | 14.9 | 18 | 9 | 14.2 | 19 | 17 | |
| 27 | 21 | 10 | 16.5 | 22 | 13 | 18.1 | 18 | 11 | 14.9 | 25 | 14 | |
| 28 | 24 | 7 | 17.7 | 23 | 13 | 18.7 | 22 | 12 | 17.7 | 20 | 10 | |
| 29 | 22 | 9 | 16.8 | 23 | 12 | 18.3 | 28 | 10 | 21.0 | 18 | 10 | |
| 30 | 20 | 9 | 15.5 | 21 | 11 | 16.8 | 22 | 11 | 17.4 | | | |
| 31 | | | | 23 | 10 | 17.7 | 23 | 14 | 19.0 | | | |